Input data and parameter estimates for ecosystem models of the southern Gulf of St. Lawrence (mid-1980s and mid-1990s)

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ABSTRACT

Savenkoff, C., H. Bourdages, D.P. Swain, S.-P. Despatie, J.M. Hanson, R. Méthot, L. Morissette, and M.O. Hammill. 2004. Input data and parameter estimates for ecosystem models of the southern Gulf of St. Lawrence (mid-1980s and mid-1990s). Can. Tech. Rep. Fish. Aquat. Sci. 2529: vi+105 pp.

Several groundfish stocks have collapsed in many areas of the northwest Atlantic over the last ten years. Mass-balance models are being used to reconstruct trophic flows through one of the areas, the southern Gulf of St. Lawrence ecosystem (NAFO division 4T) before (mid-1980s) and after (mid-1990s) the collapse of cod stock. The whole-system model of the southern Gulf of St. Lawrence is divided into 30 functional groups or compartments from phytoplankton and detritus to marine mammals and seabirds, including harvested species of pelagic, demersal, and benthic domains. We present here details of the input data (biomass, production, consumption, export, and diet composition) for each compartment used in the modelling. The successful development of ecosystem models proposed by the Comparative Dynamics of Exploited Ecosystems in the Northwest Atlantic (CDEENA) program will provide powerful new tools to evaluate the impact of human and environmental factors on a variety of Atlantic shelf ecosystems.

RÉSUMÉ

Savenkoff, C., H. Bourdages, D.P. Swain, S.-P. Despatie, J.M. Hanson, R. Méthot, L. Morissette, and M.O. Hammill. 2004. Input data and parameter estimates for ecosystem models of the southern Gulf of St. Lawrence (mid-1980s and mid-1990s). Can. Tech. Rep. Fish. Aquat. Sci. 2529: vi+105 pp.

Plusieurs stocks de poissons de fond se sont effondrés dans de nombreuses régions du nord-ouest atlantique dans les dix dernières années. Des modèles d'équilibre de masse ont été utilisés pour représenter les flux trophiques d'une de ces régions, l'écosystème du sud du Golfe du Saint-Laurent (division 4T de l'OPANO) avant (milieu des années 1980) et après (milieu des années 1990) l'effondrement du stock de morue. L'écosystème du sud du Golfe du Saint-Laurent a été divisé en 30 groupes ou compartiments trophiques depuis le phytoplancton et les détritus jusqu'aux oiseaux et mammifères marins incluant les espèces commerciales des domaines pélagique, démersal et benthique. Nous présentons ici le détail des données (biomasse, production, consommation, export et composition alimentaire) pour chaque groupe utilisé dans les modélisations. Le succès de l'élaboration des modèles écosystémiques proposés par le programme « Comparative Dynamics of Exploited Ecosystems in the Northwest Atlantic » (CDEENA) apportera de nouveaux outils scientifiques puissants pour évaluer l'impact des facteurs humains et environnementaux dans différents écosystèmes côtiers de l'Atlantique.

PREFACE

This work was supported by a multidisciplinary and inter-regional program known as CDEENA (Comparative Dynamics of Exploited Ecosystems in the Northwest Atlantic). CDEENA originally proposed a comparative analysis of changes in the structure and function of northwest Atlantic shelf ecosystems to determine how these may have affected the productivity of living resources. To this end, CDEENA brought together the expertise of field scientists and modellers to: (1) describe the changes in time and space, (2) identify and fill critical data gaps in the knowledge base, and (3) develop models to investigate ecosystem-level hypotheses (i.e., environmental variation, predation, fishing effects) concerning changes in reproduction, mortality, growth, and feeding of cod and other species.

The ecosystems that have been studied are the Newfoundland Shelf (NAFO 2J3KLNO), the northern Gulf of St. Lawrence (NAFO 4RS), the southern Gulf of St. Lawrence (NAFO 4T), and the eastern Scotian Shelf (NAFO 4VsW). CDEENA focused on two periods: (1) the mid-1980s, prior to the groundfish collapses of the early 1990s in virtually all areas, and (2) the mid-1990s, when the collapsed groundfish stocks failed to recover following fishery closures in most areas. The program tested the hypothesis that the failure of the collapsed fish stocks to recover in the 1990s was explained by changes in the ecosystems of the NW Atlantic (e.g., changes in trophic structure) driven by a combination of biological, fishing, and environmental variation.

INTRODUCTION

During the early 1990s, cod stocks in Atlantic Canada collapsed, resulting in a moratorium on fishing for many stocks throughout eastern Canada. Ten years later this moratorium remains in place, with many stocks showing little sign of recovery (Rice and Rivard 2003). The collapse of these cod stocks has generally been attributed to overfishing (Sinclair and Murawski 1997). In the case of southern Gulf of St. Lawrence cod, the recruitment rate declined from the unusually high levels observed from the mid-1970s to the early 1980s (Swain and Sinclair 2000), the natural mortality of adults increased in the 1980s (Sinclair 2001), and adult size-at-age declined from the late 1970s to the mid 1980s (Sinclair et al. 2002). Like other Atlantic cod stocks, the southern Gulf of St. Lawrence stock has shown little sign of recovery since its collapse in the early 1990s (Chouinard et al. 2003) and was placed under moratorium again in April 2003 following the opening of a small directed fishery in 1999. Stock assessment of northwest Atlantic cod stocks has followed a single-species approach, where abundance is evaluated using virtual population analysis incorporating catch data from the commercial fishery and research vessel surveys. However, a multispecies or ecosystem approach is needed to understand the factors affecting the population dynamics of cod and the failure of stocks to recover following fishery closures. The widespread nature of the cod stock collapses in the northwest Atlantic and their failure to recover suggest that common factors may be involved. One possibility is that changes in the structure and functioning of the shelf ecosystems in the northwest Atlantic are involved in the failure of these cod stocks to recover. Consequently, the Department of Fisheries and Oceans developed a multi-year research program entitled "Comparative Dynamics of Exploited Ecosystems of the Northwest Atlantic" (CDEENA) to examine changes that might have occurred in the northwest Atlantic ecosystems over the last 15 years. The objective was to develop individual ecosystem models for the northern Gulf of St. Lawrence (Northwest Atlantic Fisheries Organization [NAFO] divisions 4RS), the southern Gulf of St. Lawrence (NAFO division 4T), the Newfoundland and Labrador coast and offshore region (NAFO divisions 2J3KLNO), and the eastern Scotian Shelf region off the coast of Nova Scotia (NAFO divisions 4VsW) just prior to the cod collapses in the mid-1980s and also the mid-1990s, when the collapsed cod stocks failed to recover (Figure 1).

Here we present the data and input parameters used to construct inverse and Ecopath models of the southern Gulf of St. Lawrence ecosystem (NAFO division 4T) during the pre- (1985–1987) and post- (1994–1996) collapse periods. The inverse model was useful to obtain a first balanced solution using an objective least-squares criterion. In inverse modelling, different approaches (comparisons of different flow networks, random perturbations, sensitivity tests, etc.) were applied to assess the solution's robustness to variations in the data, as well as to provide an overall view of the ecosystem, to identify robust patterns, and to determine the location of uncertainties in the food web. The final solution of inverse modelling was the mean of 31 balanced random perturbations (including a response without perturbation). An Ecopath model was then constructed using this final solution to estimate important ecological indices (e.g., mean trophic level of the catches, trophic levels assigned to individual compartments, connectance, and omnivory). The Ecopath solution was also used in dynamic simulations between time periods using Ecopath with Ecosim software (Christensen et al. 2000). The estimates by inverse modelling are also shown for comparisons.

MATERIAL AND METHODS

Model structure

Under the steady-state assumption, consumption, representing the input, must balance the sum of the outputs consisting of, e.g., production, respiration, and egestion (non-assimilated food, feces, or detrital flow) for each individual compartment. Consumption represented ingestion of prey both within and outside the system (i.e., import).

Consumption = production + egestion + respiration (1)

Production of a given group included biomass accumulation as well as the biomass lost to natural mortality (predation, disease, and other natural causes of death) and export. Export from a group consisted of catches (fishing mortality) and net migration (migration out of or into the study area, food intake of predators that are not part of the system, etc.).

Production = biomass accumulation + predation + other mortality + export (2)

Assuming that there were no year-to-year changes in biomass during each of the two studied time periods and that net migration was zero, production was simply the biomass lost to predation, natural mortality other than predation, and fishing mortality. Finally, the general mass-balance equation for individual compartments can be written as:

Consumption - egestion - respiration - predation - other mortality - fishing mortality = $0 + \varepsilon$ (3)

The equations calculated for this study were not "absolutely" balanced, that is, the sum of the inputs and outputs for each compartment did not necessarily equal zero. We refer to these differences as residuals, which are represented by the error term ε. Inverse modelling can thus find a solution that was not necessarily balanced (not in steady state).

For phytoplankton and detritus, the general mass-balance equation was simplified. For the phytoplankton group, the net (corrected for respiration) production must balance the sum of the outputs (phytoplankton mortality including the egestion term and consumption of phytoplankton). For the detritus group, the inputs (egestion and other natural causes of death for other groups) must balance the sum of the outputs (consumption of detritus, bacterial remineralization of detritus, and burial). As bacteria were considered part of the detritus, detritus are assumed to respire.

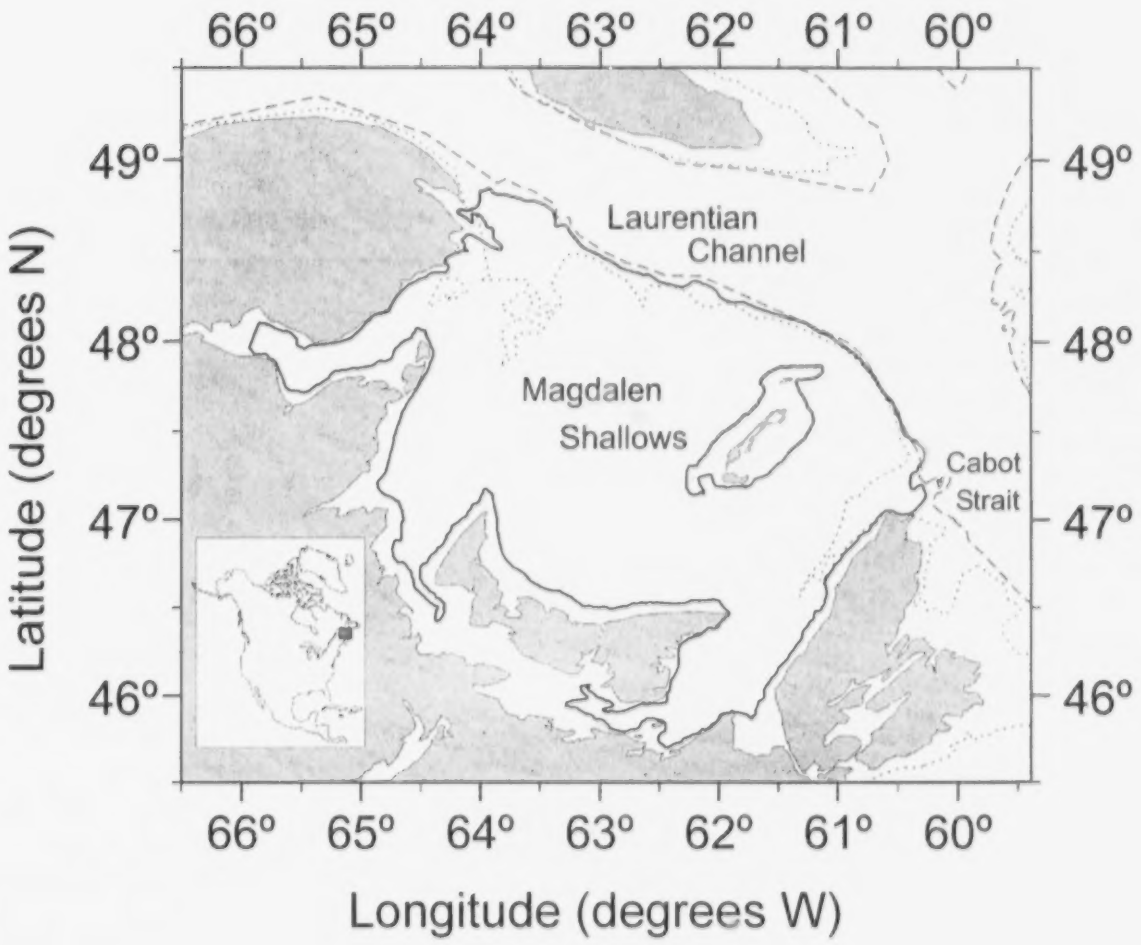

Figure 1. Study area (solid line) in the southern Gulf of St. Lawrence (NAFO division 4T) between 15 and 200 m deep equivalent to a total area of 64,075 km^2. The St. Lawrence Estuary was not included in this study. Dashed line: 200-m contour, dotted line: 100-m contour.

With the compartmental mass-balance equations, the general structure of an inverse model also includes data equations and constraints. The data equations attempt to fix the value of certain flows or combination of flows (e.g., incorporate the observations into the model that coincide with the period/region for which a solution was tested) while the constraints incorporate general knowledge into the model. The input data introduced directly into the model as data equations included values for exports (catches) from the system, production, and diet proportions locally estimated from field studies. We also used data equations for other diet proportions available only as point estimates (no variance) or with low observed values (i.e., <0.5%) and low uncertainty (i.e., SD < 0.6%). Also, when the coefficient of variation (= standard deviation/mean) of a diet proportion was high (i.e., CV > 700%), the mean was used in the data equation. The system of equations above was strongly underdetermined, so additional constraints (other conditions that reflect our prior knowledge of this system) were added to obtain a meaningful solution. Each flow was taken to be non-negative, and the flows and ratios of flows (metabolic efficiencies) were assumed to fall within certain ranges to satisfy basic metabolic requirements. Gross growth efficiency (GE) is the ratio of production to consumption and for most groups should have values between 10 and 30% (Christensen and Pauly 1992). Exceptions are top predators, e.g., marine mammals and seabirds, which can have lower GE (between 0.1 and 1%), and small, fast growing fish larvae or nauplii or bacteria, which can have higher GE (between 25 and 50%) (Christensen and Pauly 1992). Following Winberg (1956), 80% of the consumption was assumed to be physiologically useful for carnivorous fish groups while non-assimilated food (20%, consisting of urine and feces) was directed to the detritus. For herbivores, the proportion not assimilated could be considerably higher, e.g., up to 40% in zooplankton (Christensen and Pauly 1992). We constrained the assimilation efficiency (AE) to fall between 70 and 90% for all groups except for large and small zooplankton (between 50 and 90%).

Certain flows have a minimal and maximal value imposed (export for detritus, production, consumption, diet composition, etc.). The production and consumption values that were not estimated from local field studies were incorporated as constraints. The other diet proportions with higher values (i.e., >0.5%) were also specified as constraints. To facilitate comparisons with Ecopath models, we added constraints on the ecotrophic efficiency (EE). The ecotrophic efficiency is the fraction of the production that is either passed up the food web or exported. These values should be between 0 and 0.95 (Christensen and Pauly 1992, 1998). Here, a value only slightly above zero indicates that the group is not consumed in noticeable amounts by any other group in the system (e.g., top predators). Conversely, a value near or equal to 0.95 indicates that the group is heavily preyed upon and/or highly exploited by a fishery, leaving no individuals to die of other causes (small prey organisms).

The inverse model was useful to obtain a first balanced solution using an objective least-squares criterion (Savenkoff et al. 2001). In inverse modelling, different approaches (comparisons of different flow networks, random perturbations, sensitivity tests, etc.) were applied to assess the solution's robustness to variations in the data as well as to provide an overall view of the ecosystem, to identify robust patterns, and to determine the location of uncertainties in the food web. Finally, the final solution of inverse modelling was the mean of at least 31 balanced random perturbations (including a response without perturbation).

Study area

The study covers a 64,075 km^2 area of the southern Gulf of St. Lawrence (NAFO division 4T) in water with depths between 15 and 200 m (survey strata 416-438, excluding stratum 425) (Fig. 1). Infra-littoral species and American lobster (*Homarus americanus*) were not included in this study. This zone was excluded from the model because exchanges between infra-littoral and pelagic zones are still poorly understood. The periods covered by this analysis are the pre-collapse (mid-1980s: 1985-1987) and post-collapse (mid-1990s: 1994-1996) periods for cod stocks in most areas of the northwest Atlantic.

Catches in the deep strata of the Laurentian channel (415, 425, and 439) were excluded from this analysis. This applies to all biomass estimates from the survey.

Functional groups

Based on data availability and the ecological and commercial significance of the species, the whole-system model of the southern Gulf of St. Lawrence was divided into 30 functional groups or compartments representing the main pelagic, demersal, and benthic species (Table 1). We distinguished five marine mammal groups, one seabird group, fourteen fish groups, eight invertebrate groups, one phytoplankton group, and one detritus group (Table 1). Some groups such as large pelagic feeders and large demersal feeders are composite groups, where the species were aggregated on the basis of similarity of size and ecological role. Atlantic cod (*Gadus morhua* L.) and American plaice (*Hippoglossoides platessoides*) were each separated into two groups based on diet, age/size at first capture in the fishery, and age/size at maturity. Smaller fish prey mainly on invertebrates while larger fish feed mainly on fish. These changes tend to occur gradually with increasing length, but for these models it was assumed that the change occurs at 35 cm for Atlantic cod (Lilly 1991) and American plaice (Pitt 1973). Due to a lack of data (e.g., diet composition, production, and consumption), we could not distinguish juveniles and adults for other fish species. Finally, bacteria were considered part of the detritus compartment (Table 1).

Table 1. Functional groups used in modelling for both periods in the southern Gulf of St. Lawrence.

Group Name	Main species
Cetaceans	*Balaenoptera physalus*, *Balaenoptera acutorostrata*, *Megaptera novaeangliae*, *Phocoena phocoena*, *Lagenorhynchus acutus*, *Lagenorhynchus albirostris*
Harp seals	*Phoca groenlandica*
Hooded seals	*Cystophora cristata*
Grey seals	*Halichoerus grypus*
Harbour seals	*Phoca vitulina*
Seabirds	*Phalacrocorax carbo*, *Phalacrocorax auritus*, *Larus delwarensis*, *L. argentatus*, *L. marinus*, *Sterna hirundo*, *S. paradisaea*, *Cepphus grylle*, *Oceanodroma leucorhoa*, *Morus bassanus*, *Rissa tridactyla*, *Uria aalge*, *Alca torda*, *Fratercula arctica*
Large Atlantic cod (> 35 cm)	*Gadus morhua*
Small Atlantic cod (≤ 35 cm)	*Gadus morhua*
Greenland halibut	*Reinhardtius hippoglossoides*
Small American plaice (≤ 35 cm)	*Hippoglossoides platessoides*
Large American plaice (> 35 cm)	*Hippoglossoides platessoides*
Flounders	*Limanda ferruginea*, *Glyptocephalus cynoglossus*, *Pseudopleuronectes americanus*
Skates	*Amblyraja radiata*, *Malacoraja senta*, *Leucoraja ocellata*
Redfish	*Sebastes mentella*, *Sebastes fasciatus*
Large demersal feeders	*Urophycis tenuis*, *Melanogrammus aeglefinnus*, *Centroscyllium fabricii*, *Anarhichas* spp., *Cyclopterus lumpus*, *Lycodes* spp., Macrouridae, Zoarcidae, *Lophius americanus*, *Hippoglossus hippoglossus*
Small demersal feeders	*Myoxocephalus* spp., *Tautogolabrus adspersus*, *Macrozoarces americanus*, large demersal juveniles
Capelin	*Mallotus villosus*
Large pelagic feeders	*Squalus acanthias*, *Pollachius virens*, *Merluccius bilinearis*, *Cetorhinus maximus*

Table 1. Cont.

Group Name	Main species
Piscivorous small pelagic feeders	*Scomber scombrus*, piscivorous myctophids and other mesopelagics, *Illex illecebrosus*, piscivorous large pelagic juveniles
Planktivorous small pelagic feeders	*Clupea harengus harengus*, planktivorous myctophids and other mesopelagics, *Scomberesox saurus*, *Gonatus* sp., planktivorous large pelagic juveniles
Shrimp	*Argis dentata*, *Eualus macilentus*, *E. gaimardi*, *Pandalus montagui*
Large crustaceans	*Chionoecetes opilio*, other non-commercial species (*Hyas* spp.)
Echinoderms	*Echinarachnius parma*, *Stronglyocentrotus pallidus*, *Ophiura robusta*
Molluscs	*Mesodesma deauratum*, *Cyrtodaria siliqua*
Polychaetes	*Exogene hebes*
Other benthic invertebrates	Miscellaneous crustaceans, nematodes, other meiofauna
Large zooplankton (> 5 mm)	Euphausiids, chaetognaths, hyperiid amphipods, cnidarians and ctenophores (jellyfish), mysids, tunicates >5 mm, ichthyoplankton
Small zooplankton (< 5 mm)	Copepods (mainly *Oithona similis*, *Temora longicornis*, *Pseudocalanus* spp., and *Calanus finmarchicus*), tunicates < 5 mm, meroplankton, heterotrophic protozoa (flagellates, dinoflagellates, and ciliates)
Phytoplankton	Diatom species such as *Chaetoceros affinis*, *Chaetoceros* spp., *Leptocylindrus minimus*, *Thalassiiosira nordenskioldii*, *T. spp.*, *Fragilariopsis* spp., and a mixture of autotrophic and mixotrophic organisms including Cryptophytes, dinoflagellates, Prasinophytes, and Prymnesiophytes
Detritus	Sinking particulate organic matter including both large particles (consisting of animal carcasses and debris of terrigenous and coastal plants) and fine particles (mostly from planktonic organisms, including feces, moults, phytoplankton aggregates, bacteria)

Collecting the data

All the parameter estimations were made within a collaborative approach, in which experts for the various functional groups were consulted. Considerable effort was expended to obtain input data in the study area and during the periods of interest. However, information on several groups (e.g., benthic invertebrates and zooplankton) was sparse or non-existent for the area and periods studied, and was thus taken from the literature or for the same area but another time period. Based on these different sources of data (local and literature), we estimated the lower and upper limits of each input data used in inverse modelling. This process partly explains the high coefficients of variation for the production, consumption, and diet data (mid-1980s: 71, 86, and 224%, respectively, and mid-1990s: 73, 85, and 461%, respectively) as well as those for biomass or export (mid-1980s: 56 and 50%, respectively, and mid-1990s: 56 and 60%, respectively).

Biomass

The biomass density (called biomass in this document) of a species (or group of species) was assumed to be constant within each of the two periods modelled. The biomass of each box of the model was obtained directly or was estimated from similar ecosystems when it was not available for 4T. This parameter is expressed in biomass per unit area (e.g., tons wet weight km^{-2}). Biomass was estimated from sequential population analysis or scientific trawl survey data for most groups in the model.

Biomass estimates for fish species were based on catches in a bottom-trawl survey conducted in the southern Gulf each September. Different species have different degrees of catchability by the survey fishing gear, making comparison of biomass estimates difficult at best. Trawlable biomass estimates were thus converted to catchability-adjusted biomass based on catchability relationships estimated by Harley and Myers (2001). Length-specific corrections were applied to numbers-at-length data before they were converted to biomass estimates. In this way, we hoped to lessen the impact of catchability on the biomass estimates and render data comparable between species (Table 2).

Standard deviations for biomass and catch were based only on the variations in the point estimates for the three years in each period (i.e., the error in the estimates themselves was not included in these SDs).

Table 2. Catchability factors (Q) used to estimate biomass of fish species from trawl data. L: length in cm.

Species or species group	Catchability coefficient	Associated species
Cod	$Q = \frac{0.949 * \exp(-5.06 + 0.139 * L)}{1 + \exp(-5.06 + 0.139 * L)}$	
Haddock	$Q = \frac{1.59 * \exp(-2.77 + 0.0646 * L)}{1 + \exp(-2.77 + 0.0646 * L)}$	
Demersal gadoids	$Q = \frac{1.04 * \exp(-3.47 + 0.0914 * L)}{1 + \exp(-3.47 + 0.0914 * L)}$	Grenadiers, fourbeard rockling, eelpouts, longfin hake, white hake, large headed (L x 1.25; sculpins, lumpfish, wolffish, sea raven), small headed (L x 0.75; seasnails, spiny lumpsucker)
Pelagic gadoids	$Q = \frac{0.64 * \exp(-4.58 + 0.0785 * L)}{1 + \exp(-4.58 + 0.0785 * L)}$	Spiny dogfish, silver hake, pollock, redfish (L x 1.25)
Flatfish	$Q = \frac{0.986 * \exp(-4.43 + 0.109 * L)}{1 + \exp(-4.43 + 0.109 * L)}$	Greenland halibut, American plaice, flounders, skates (L x 1.25)

Production

Production is the total amount of tissue produced in the population or community under study during a given time period (Christensen and Pauly 1992). It includes all living matter produced by a group (even if it's finally consumed, fished, or lost by other mortality) during the model period. In the southern Gulf of St. Lawrence model, it was assumed that there was no year-to-year change in biomass within each time period and that emigration was zero. Thus production in this model is simply the biomass that is lost to natural mortality (predation, disease, and other natural causes of death) and fishing mortality. P/B is the ratio of production (P) to biomass (B). Absolute production is a flux expressed in biomass per unit area per year (e.g., t km^{-2} yr^{-1}).

The means and SDs were based on (1) the two extreme values (when different approaches were used to calculate them and using biomass values from the three years) or (2) all the point estimates (when a single approach was used and using biomass values from the three years).

Consumption

Consumption is defined as the utilization of food by a group during the time period considered by the model (Christensen and Pauly 1993). Q/B is the ratio of consumption (Q) to biomass (B). Absolute consumption is a flux expressed in biomass per surface area per year (e.g., $t\ km^{-2}\ yr^{-1}$).

Consumption was estimated from field studies where possible, either from the region or for species from similar areas reported in the literature. In addition, models were used to estimate consumption by marine mammals (Hammill and Stenson 2000) and seabirds (G. Chapdelaine, Environment Canada, Migratory Birds Division, Sainte-Foy, Québec, unpublished data).

Where it was not possible to do either, consumption values were taken either from the literature and/or estimated assuming a gross growth efficiency (GE; the ratio of production to consumption) ranging between 10 and 30% (Christensen and Pauly 1992).

The means and SDs were calculated on the two extreme values.

Diet composition

Diet matrices were constructed using field data from the study area whenever possible. However, these data do not exist for some species. For these species, diet data were taken for the same area but for another time period or from the literature for other areas and/or time periods. Using all the available field samples or literature reports, the minimum and maximum values observed for each diet proportion were used as inputs for inverse modelling. Means and standard deviations were calculated either directly from the lower and upper limits when there was no information on number of stomachs (mean and SD of the two extreme values) or from the different diet proportions, which were weighted by the number of stomachs when stomach content analyses were given (mean and SD of all the point estimates). The diet outputs estimated by the balanced (optimized) solution of inverse modelling were then used as inputs for the Ecopath model. In the diet tables, empty cells indicate that a prey item was never found whereas "0.0" indicates that it was found in very small amounts (<0.1%) or that this represented a potential trophic relation between prey and predator in other ecosystems or another period of time (equal to 0%). There was a large number of such values during the mid-1980s (57 out of 282 flows) and the mid-1990s (67 of 282 flows).

FishBase

Occasionally, information was not available for some parameters. When this happened we referred to FishBase (Froese and Pauly 2002), which is a biological database developed at the International Centre for Living Aquatic Resources Management (ICLARM) in collaboration with FAO and other organizations. It includes information on fish species and is updated frequently with regards to information such as maximum size, growth parameters, natural mortality, and standardized diet composition (Froese and Pauly 1995).

RESULTS: DATA GATHERING AND SYNTHESIS

In this section, each functional group of the southern Gulf of St. Lawrence ecosystem is described along with respective estimates of biomass, production, consumption, and diet composition that are used as inputs for modelling in both periods.

Cetacea

Background

The southern Gulf of St. Lawrence is dominated by boreal cetaceans ranging from large and medium-sized mysticetes and odontocetes to small odontocetes such as porpoises and dolphins (Kingsley and Reeves 1998). Minke (*Balaenoptera acutorostrata*) and long-finned pilot (*Globicephala melas*) are the most abundant species among the large and medium whales. White-sided dolphins (*Lagenorhynchus acutus*) are the most abundant of the small dolphins in the southern Gulf while the harbour porpoise (*Phocoena phocoena*) also occurs in this area (Kingsley and Reeves 1998). The cetacean survey of the Gulf of St. Lawrence (Kingsley and Reeves 1998) covered 221,950 km^2, so we used this inventory area to calculate the parameters for this group instead of the value habitually used for the other groups (the sampling area for division 4T).

Catch

Canada ceased commercial whaling in 1972 and there has been no hunt for subsistence purposes in 4T. However, information from a questionnaire survey conducted in 1989 and 1990 in the Gulf (4RST) indicated an annual average incidental catch from fishing gear of 1,835 harbour porpoises (Fontaine et al. 1994a). This is equivalent to a catch of 92 tons within a 221,950 km^2 sampling area ($3.75 \times 10^{-4} \pm 2.09 \times 10^{-5}$ t km^{-2} yr^{-1}) for both periods. The final solution of inverse modelling (hereafter termed "inverse solution") estimated a catch of 3.71×10^{-4} and 3.78×10^{-4} km^{-2} yr^{-1} for the mid-1980s and mid-1990s, respectively.

Biomass

Aerial survey estimates of cetacean abundance in the Gulf of St. Lawrence, not corrected for visibility bias, are available for the summer of 1995 (Kingsley and Reeves 1998). The area of the strata corresponding to the southern Gulf covers 77,482 km^2. The density in this zone is applied to the present study zone. These estimates were adjusted by a factor of 1.09 to account for animals that were potentially visible to the observers but were not seen (Marsh and Sinclair 1989) and by a factor of 2.27 to account for animals missed owing to water turbidity (Marsh and Sinclair 1989). These adjustments resulted in abundance estimates of 396 (SE = 223) minke whales, 891 (SE = 693) long-finned pilot whales, 11,629 (SE = 11,233) Atlantic white-sided dolphins, and 8,512 (SE = 4,058) harbour porpoises in 1995. Based on these abundance

estimates, we used growth rate and mean body mass for each species to back-calculate (1985, 1986, 1987, and 1994) or estimate (1996) biomass values for each period.

Mean body mass taken from the literature was 5.6 t for minke whales, 1.4 t for long-finned pilot whales, and 0.05 t for harbour porpoises (averaged from Lien [1985], Martin [1990], and Kenney et al. [1997]), and 0.13 t for white-sided dolphins (Sergeant et al. 1980). To calculate biomass, we used a population growth rate of 6.7% for minke whales (Bundy et al. 2000), 4.0% for long-finned pilot whales (Waring et al. 1999), 9.0% for harbour porpoises (Caswell et al. 1998), and 2.0% for white-sided dolphins (Heise 1997). For harbour porpoises, an annual incidental catch of 581 individuals was also used. Assuming a residence time of 180 days for all whales within the potential area of Kinglsley and Reeves (1998) (77,482 km^2), the average annual biomass was 0.024 ± 0.001 and 0.034 ± 0.001 t km^{-2} in the mid-1980s and mid-1990s, respectively.

Production

Production was assumed to be equivalent to the biomass multiplied by natural mortality plus catch. Natural mortality for a combination of cetaceans was estimated at 0.074 (Ohsumi 1979; Tanaka 1990) and the mean annual catch used was 3.75×10^{-4} t km^{-2} yr^{-1} (Fontaine et al. 1994a). This resulted in a total annual production of 0.002 and 0.003 t km^{-2} yr^{-1} during the mid-1980s and mid-1990s, respectively. The inverse solution estimated a production of 0.001 t km^{-2} yr^{-1}, representing a P/B of 0.060 yr^{-1} in the mid-1980s, while production and P/B estimates were 0.003 t km^{-2} yr^{-1} and 0.085 yr^{-1}, respectively, in the mid-1990s.

Consumption

The daily consumption by cetaceans was calculated using:

$$R = 0.1W^{0.8} \quad (4)$$

where R is the daily ration for an individual in kg and W is the mean body mass in kg (Trites et al. 1997). Assuming a residence time of 180 days, the annual consumption by species for the mid-1980s and mid-1990s were 0.051 and 0.092 t km^{-2} yr^{-1} for minke whales, 0.048 and 0.068 t km^{-2} yr^{-1} for long-finned pilot whales, 0.039 and 0.045 t km^{-2} yr^{-1} for harbour porpoises, and 0.111 and 0.133 t km^{-2} yr^{-1} for Atlantic white-sided dolphins, respectively. This gives a mean annual consumption of 0.249 ± 0.008 t km^{-2} yr^{-1} (range: 0.242–0.257 t km^{-2} yr^{-1}) and 0.338 ± 0.012 t km^{-2} yr^{-1} (range: 0.326–0.350 t km^{-2} yr^{-1}) during the mid-1980s and mid-1990s, respectively. Gross growth efficiency (GE = P/Q) ranges between 0.1 and 1% for marine mammals (Christensen and Pauly 1992). Based on the previous total annual production (0.002 and 0.003 t km^{-2} yr^{-1}) and the GE limits, we obtained other consumption values of 0.215 and 2.149 t km^{-2} yr^{-1} and 0.293 and 2.933 t km^{-2} yr^{-1} for the two periods, respectively. The values based on the lower GE limit were not realistic, so the resulting consumption ranges were 0.215 and 0.257 t km^{-2} yr^{-1} (mean: 0.236 ± 0.030 t km^{-2} yr^{-1}) and 0.293 and 0.350 t km^{-2} yr^{-1} (mean: 0.322 ± 0.040 t km^{-2} yr^{-1}) during the mid-1980s and mid-1990s, respectively. The inverse solution estimated a consumption

of 0.219 t km^{-2} yr^{-1}, representing a Q/B of 9.178 yr^{-1} during the mid-1980s, while consumption and Q/B estimates were 0.302 t km^{-2} yr^{-1} and 8.789 yr^{-1}, respectively, in the mid-1990s.

Diet composition

Unfortunately, there are few quantitative descriptions of diet for cetaceans. Where the literature refers to prey using terms such as "preponderant" or "predominant," it was assumed that they make up at least 75% of consumption by weight. If other prey were reported, remaining consumption was divided equally among them. Based on the literature, the following diets were used in the analysis:

- Minke whales: capelin, small cod, herring, squid, and euphausiids (Horwood 1990);
- Long-finned pilot whales: squid, juvenile cod, and capelin (Lien 1985);
- Harbour porpoises: capelin, herring, redfish, mackerel, cod, squid, and sand lance (Fontaine et al. 1994b);
- White-sided dolphins: herring, squid, smelt, silver hake, and crustaceans (Katona et al. 1978).

In order to calculate the overall proportion of each prey item by mass, total consumption by prey type was first calculated and overall proportions weighted according to the consumption of each cetacean species (Table 3).

Table 3. Diet composition of cetaceans used in modelling for each period. Est: diet estimates by the inverse model; TRN: number of trophic relations; SD: standard deviation. All values are percentages except TRN. Empty cells indicate that a prey item was never found whereas "0.0" indicates that it was found in very small amounts. Groups with indicated CV (available only as point estimates): Min = mean – (mean x 60%), Max = mean + (mean x 60%). Values used in data equations or as upper and lower limit constraints are indicated in boldface.

	Cetaceans (mid-1980s) (CV = 60%)				
Prey	Mean	±SD	Min	Max	Est
Large cod	**0.0**		0.0	0.1	0.0
Small cod	1.1		**0.4**	**1.7**	1.3
Green. halibut					
Small American plaice	**0.0**		0.0	0.0	0.0
Large American plaice	**0.0**		0.0	0.0	0.0
Flounders					
Skates					
Redfish	**0.9**		0.4	1.5	0.9
Large demersals	**0.0**		0.0	0.0	0.0
Small demersals	**0.0**		0.0	0.0	0.0
Capelin	21.7		**8.7**	**34.8**	18.7
Large pelagics	2.2		**0.9**	**3.6**	1.6
Pisci. small pelagics	41.4		**16.5**	**66.2**	40.5
Plank. small pelagics	30.2		**12.1**	**48.4**	34.1
Shrimp	**0.7**		0.3	1.1	0.7
Large crustacea					
Echinoderms					
Molluscs					
Polychaetes					
Other bent. inver.					
Large zooplankton	1.7		**0.7**	**2.7**	2.1
Small zooplankton					
Phytoplankton					
Detritus					
Total	100.0		40.0	160.0	100.0
TRN	13				

Table 3. Cont.

	Cetaceans (mid-1990s) (CV = 60%)				
Prey	Mean	±SD	Min	Max	Est
Large cod	**0.0**		0.0	0.1	0.0
Small cod	1.4		**0.6**	**2.2**	0.7
Green. halibut					
Small American plaice	**0.0**		0.0	0.0	0.0
Large American plaice	**0.0**		0.0	0.0	0.0
Flounders					
Skates					
Redfish	**0.8**		0.3	1.3	0.8
Large demersals	**0.0**		0.0	0.0	0.0
Small demersals	**0.0**		0.0	0.0	0.0
Capelin	25.8		**10.3**	**41.2**	30.0
Large pelagics	2.0		**0.8**	**3.1**	2.4
Pisci. small pelagics	40.2		**16.1**	**64.2**	34.9
Plank. small pelagics	27.3		**10.9**	**43.7**	28.3
Shrimp	**0.6**		0.2	0.9	0.6
Large crustacea					
Echinoderms					
Molluscs					
Polychaetes					
Other bent. inver.					
Large zooplankton	1.9		**0.8**	**3.1**	2.2
Small zooplankton					
Phytoplankton					
Detritus					
Total .	100.0		40.0	160.0	100.0
TRN	13				

Seals

Background

Four species of pinnipeds are common in the Gulf of St. Lawrence. The harp seal (*Phoca groenlandica*) is the most abundant pinniped in Atlantic Canada and usually summers in the Canadian Arctic or northwest Greenland before returning south to winter in Canadian Atlantic waters. Reproduction occurs in March on the pack ice in the Gulf of St. Lawrence (Gulf herd) and off southern Labrador (Front herd). In the Gulf, animals whelp in two areas: off the lower North Shore and near the Îles-de-la-Madeleine (Sergeant 1991). The northwest Atlantic population was estimated to be 3,457,129 and 5,037,255 during the mid-1980s and mid-1990s, respectively

(Healey and Stenson 2000), with an average of 4.2% of the pups, 4.2% of juveniles, and 6.9% of the adults found in the southern Gulf of St Lawrence (Hammill and Stenson 2000).

Hooded seals (*Cystophora cristata*), which are larger than harp seals, are the least abundant pinniped within the study area, with an average population of 8,698 and 13,459 individuals for 1985–1987 and 1994–1996, respectively (M. Hammill, unpublished data). Only 18.1% of the animals are situated in division 4T (Hammill and Stenson 2000). In the northwest Atlantic, most pups are born in March on pack ice off northeast Newfoundland, with smaller whelping concentrations located in Davis Strait and the Gulf of St. Lawrence. After leaving the whelping patch in late March, adults from the Gulf of St. Lawrence move to the northern Gulf where they remain until mid-May, when they return to Greenland. Hooded seals have been protected in the Gulf since 1972 (Hammill et al. 1997).

The grey seal (*Halichoerus grypus*) is slightly smaller than the hooded seal. Major breeding colonies in eastern Canada are located on Sable Island and in the southern Gulf of St. Lawrence (Mansfield and Beck 1977). After breeding, both juveniles and adults disperse widely over eastern Canada. Large numbers are known to feed in the southern Gulf of St. Lawrence, which makes it the second most abundant pinniped of the zone (Hammill and Stenson 2000). The population in 1985–1987 averaged 39,320 individuals from the Gulf herd and 33,386 individuals from the Sable Island herd (M. Hammill, unpublished data). The population in 1994–96 averaged 67,690 individuals from the Gulf herd and 100,263 individuals from the Sable Island herd (M. Hammill, unpublished data). Hammill and Stenson (2000) estimated that 35.1% of the Gulf herd and 4.7% of the Sable Island herd were found in division 4T for both periods.

Harbour seals (*Phoca vitulina*) are found throughout eastern Canada (Boulva and McLaren 1979), occurring in small groups dispersed along coastal areas (Lesage et al. 1995). Harbour seal abundance in Atlantic Canada has never been evaluated by direct survey. Based on questionnaires sent to fisheries officers, Boulva and McLaren (1979) estimated that there were about 13,000 animals in eastern Canada. Hammill and Stenson (2000) modelled population changes for this species and estimated that the average population was 18,305 and 30,163 for 1985–1987 and 1994–1996, respectively (M. Hammill, unpublished data), with 8.0% of animals situated in the southern Gulf (Hammill and Stenson 2000).

Catch

Commercial catches (total numbers) for harp and grey seals are reported in the Atlantic resource management landing reports (Stenson et al. 2000). Catches were divided into pups (young of the year) and animals one year and older (Sjare et al. 1996). Numbers-at-age were multiplied by mean mass-at-age (Hammill and Stenson 2000) to obtain total catches in tons. For harp seals, the mean catches were estimated at $6.39 \times 10^{-4} \pm 3.80 \times 10^{-4}$ t km^{-2} yr^{-1} and $4.91 \times 10^{-3} \pm 6.48 \times 10^{-3}$ t km^{-2} yr^{-1} for 1985–1987 and 1994–1996, respectively. The inverse solution estimated a catch of 6.52×10^{-4} and 5.60×10^{-3} t km^{-2} yr^{-1} for the mid-1980s and mid-1990s, respectively.

Hooded seals have been protected in the Gulf since 1972 (Hammill et al. 1997), so catch was assumed to be negligible.

The grey seal is not hunted commercially in Canadian waters. However, this species was subject to a scientific removal and bounty hunting. Harvesting activity has declined over the last

50 years and the bounty was eliminated in 1992 (Hammill et al. 1998). These removals resulted in an estimated mean annual catch of $7.17 \times 10^{-4} \pm 6.96 \times 10^{-4}$ t km^{-2} yr^{-1} and $2.46 \times 10^{-4} \pm 2.59 \times 10^{-4}$ t km^{-2} yr^{-1} for 1985–1987 and 1994–1996, respectively. The inverse solution estimated a catch of 9.06×10^{-4} and 2.44×10^{-4} t km^{-2} yr^{-1} for the mid-1980s and mid-1990s, respectively.

Even though harbour seals have been protected since 1976 (Boulva and McLaren 1979), some losses may have occurred through by-catch by commercial fisheries. However, there is no data available to assess this loss, so catch was not entered in the model.

Biomass

Biomass was estimated by multiplying abundance by mean mass-at-age (Hammill and Stenson 2000). The number of seals in each age class was obtained from an updated version of the population model of Hammill and Stenson (2000), extrapolated backwards to 1985. Biomass was adjusted for residence time in 4T (Hammill and Stenson 2000), resulting in mean annual biomass estimates for the 1985–1987 and 1994–1996 periods of 0.231 ± 0.013 and 0.347 ± 0.013 t km^{-2} for harp seals, 0.003 ± 0.000 and 0.004 ± 0.000 t km^{-2} for hooded seals, 0.028 ± 0.002 and 0.052 ± 0.002 t km^{-2} for grey seals, and 0.001 ± 0.000 and 0.002 ± 0.000 t km^{-2} for harbour seals. Note that the standard deviation for each seal group was only the variation in the point estimates for the three years in each period.

Production

The P/B ratio was estimated by dividing the pup biomass by the uncorrected population biomass (minimum value) for the southern Gulf of St. Lawrence as reported in an updated version of the population model of Hammill and Stenson (2000) for each period. Multiplying this P/B ratio by mean biomass for each species resulted in production values of 0.016 t km^{-2} yr^{-1} for harp seals, 0.0002 t km^{-2} yr^{-1} for hooded seals, 0.0018 t km^{-2} yr^{-1} for grey seals, and 0.00009 t km^{-2} yr^{-1} for harbour seals during the mid-1980s. During the mid-1990s, the production values were 0.023 t km^{-2} yr^{-1} for harp seals, 0.0002 t km^{-2} yr^{-1} for hooded seals, 0.0029 t km^{-2} yr^{-1} for grey seals, and 0.00015 t km^{-2} yr^{-1} for harbour seals.

Based on the annual consumption values of Hammill and Stenson (2000) (see below) and the upper GE limit (1%; values based on the lower GE limit of 0.1% were not realistic), we obtained other production values: 0.007 t km^{-2} yr^{-1} for harp seals, 0.0003 t km^{-2} yr^{-1} for hooded seals, 0.0020 t km^{-2} yr^{-1} for grey seals, and 0.00005 t km^{-2} yr^{-1} for harbour seals during the mid-1980s. During the mid-1990s, the production values were 0.011 t km^{-2} yr^{-1} for harp seals, 0.0005 t km^{-2} yr^{-1} for hooded seals, 0.0037 t km^{-2} yr^{-1} for grey seals, and 0.00008 t km^{-2} yr^{-1} for harbour seals.

Production was also estimated by adding annual mass gain for each age class in the population to mass of pups. Mass at age were obtain from Chabot and Stenson (2002) and Leblanc (2003) for harp seals and hooded seals, respectively. An updated version of the population model of Hammill and Stenson (2000) provided the information for grey and harbour seals. In the 1985–1987 period, this resulted in production values of 0.031 t km^{-2} yr^{-1} for harp seals, 0.0003 t km^{-2} yr^{-1} for hooded seals, 0.0062 t km^{-2} yr^{-1} for grey seals, and 0.00026 t km^{-2} yr^{-1}

for harbour seals. During the 1994–1996 period, the production values were estimated at 0.043 t km^{-2} yr^{-1} for harp seals, 0.0005 t km^{-2} yr^{-1} for hooded seals, 0.0111 t km^{-2} yr^{-1} for grey seals, and 0.00042 t km^{-2} yr^{-1} for harbour seals.

Finally, the resulting upper and lower limit ranges were of 0.007 to 0.031 t km^{-2} yr^{-1} (mean: 0.019 ± 0.016 t km^{-2} yr^{-1}) for harp seals, 0.0002 to 0.0003 t km^{-2} yr^{-1} (mean: 0.0002 ± 0.0001 t km^{-2} yr^{-1}) for hooded seals, 0.0017 to 0.0062 t km^{-2} yr^{-1} (mean: 0.0039 ± 0.0032 t km^{-2} yr^{-1}) for grey seals, and 0.00005 to 0.00026 t km^{-2} yr^{-1} (mean: 0.00015 ± 0.00015 t km^{-2} yr^{-1}) for harbour seals during the mid-1980s. During the mid-1990s, we obtained upper and lower limit ranges of 0.011 to 0.043 t km^{-2} yr^{-1} (mean: 0.027 ± 0.022 t km^{-2} yr^{-1}) for harp seals, 0.0002 to 0.0005 t km^{-2} yr^{-1} (mean: 0.0004 ± 0.0002 t km^{-2} yr^{-1}) for hooded seals, 0.0029 to 0.0111 t km^{-2} yr^{-1} (mean: 0.0070 ± 0.0058 t km^{-2} yr^{-1}) for grey seals, and 0.00008 to 0.00042 t km^{-2} yr^{-1} (mean: 0.00025 ± 0.00024 t km^{-2} yr^{-1}) for harbour seals. During the mid-1980s, the inverse solution estimated production values of 0.016 t km^{-2} yr^{-1} (P/B = 0.068 yr^{-1}) for harp seals, 0.0003 t km^{-2} yr^{-1} (P/B = 0.100 yr^{-1}) for hooded seals, 0.0047 t km^{-2} yr^{-1} (P/B = 0.166 yr^{-1}) for grey seals, and 0.00008 t km^{-2} yr^{-1} (P/B = 0.061 yr^{-1}) for harbour seals. During the mid-1990s, the inverse solution estimated production values of 0.013 t km^{-2} yr^{-1} (P/B = 0.038 yr^{-1}) for harp seals, 0.0004 t km^{-2} yr^{-1} (P/B = 0.087 yr^{-1}) for hooded seals, 0.0084 t km^{-2} yr^{-1} (P/B = 0.162 yr^{-1}) for grey seals, and 0.00014 t km^{-2} yr^{-1} (P/B = 0.067 yr^{-1}) for harbour seals.

Consumption

Total annual consumption of prey by each seal species in the study area was estimated from an updated version of the consumption model of Hammill and Stenson (2000) using seasonal feeding behaviours. The annual consumption ranges were 0.722–0.808 t km^{-2} yr^{-1} for harp seals, 0.032–0.036 t km^{-2} yr^{-1} for hooded seals, 0.110–0.309 t km^{-2} yr^{-1} for grey seals, and 0.0047–0.0052 t km^{-2} yr^{-1} for harbour seals during the mid-1980s. During the mid-1990s, we obtained ranges of 1.098 to 1.182 t km^{-2} yr^{-1} for harp seals, 0.050 to 0.055 t km^{-2} yr^{-1} for hooded seals, 0.207 to 0.551 t km^{-2} yr^{-1} for grey seals, and 0.008 to 0.009 t km^{-2} yr^{-1} for harbour seals.

Based on the maximum production values (see above) and the upper GE limit (1%; values based on the lower GE limit of 0.1% were not realistic), we obtained other consumption values: 3.054 and 4.257 t km^{-2} yr^{-1} for harp seals, 0.030 and 0.046 t km^{-2} yr^{-1} for hooded seals, 0.618 and 1.110 t km^{-2} yr^{-1} for grey seals, and 0.026 and 0.042 t km^{-2} yr^{-1} for harbour seals during the mid-1980s and mid-1990s, respectively.

Finally, based on these different values, we estimated the lower and upper consumption limits used as constraints in inverse modelling. The resulting mean consumption values of each upper and lower limit range were 1.888 ± 1.649 t km^{-2} yr^{-1} for harp seals, 0.033 ± 0.004 t km^{-2} yr^{-1} for hooded seals, 0.364 ± 0.359 t km^{-2} yr^{-1} for grey seals, and 0.015 ± 0.015 t km^{-2} yr^{-1} for harbour seals during the mid-1980s. During the mid-1990s, the mean consumption values were 2.678 ± 2.234 t km^{-2} yr^{-1} for harp seals, 0.045 ± 0.014 t km^{-2} yr^{-1} for hooded seals, 0.659 ± 0.638 t km^{-2} yr^{-1} for grey seals, and 0.025 ± 0.024 t km^{-2} yr^{-1} for harbour seals. The inverse solution estimated consumption values of 2.030 t km^{-2} yr^{-1} (Q/B = 8.793 yr^{-1}) for harp seals, 0.030 t km^{-2} yr^{-1} (Q/B = 10.871 yr^{-1}) for hooded seals, 0.508 t km^{-2} yr^{-1} (Q/B = 18.122 yr^{-1}) for grey seals, and 0.008 t km^{-2} yr^{-1} (Q/B = 6.603 yr^{-1}) for harbour seals during the mid-1980s. During the mid-1990s, the modelling estimates were 1.433 t km^{-2} yr^{-1} (Q/B = 4.127 yr^{-1}) for harp seals, 0.044 t km^{-2} yr^{-1}

($Q/B = 10.352\ yr^{-1}$) for hooded seals, 1.008 t km^{-2} yr^{-1} ($Q/B = 19.411\ yr^{-1}$) for grey seals, and 0.018 t km^{-2} yr^{-1} ($Q/B = 8.951\ yr^{-1}$) for harbour seals.

Diet composition

For harp seals, diet information was available for nearshore waters of the northwest Atlantic during 1990–1993 (Lawson et al. 1995), for inshore 2J3KL during 1991–1992 (Lawson et al. 1993), and for the St. Lawrence Estuary (Murie and Lavigne 1991; Beck et al. 1993; Lawson et al. 1995; Hammill and Stenson 2000). According to these diet studies, the main prey species were, in order of importance, capelin, Atlantic herring, and Atlantic cod. During the mid-1980s, we modified the proportion of capelin in the harp seal diet to reflect the lesser abundance of capelin in the southern Gulf (initial range: 12.4–89.8%, range used: 0.0–20.0%). Similarly, we modified the proportion of large cod in the harp seal diet to better reflect the lesser abundance of large cod in the southern Gulf (initial range: 0.0–3.9%, range used: 0.0–1.5%) during the mid-1990s (M. Hammill, unpublished data).

There was no diet information available for hooded seals in the Gulf. Hammill et al. (1997) used a diet based on work done by Ross (1993), where the main prey items were young Greenland halibut, flounders, and small pelagic feeders. Other information about this species was based on offshore samples from NAFO divisions 2J3KL collected from 1991–1993 (Lawson et al. 1993). In that study, examined stomachs contained mainly Atlantic cod, witch flounder, and squid. Hammill and Stenson (2000) used a diet made up of samples from Ross (1993) and Lawson and Stenson (DFO, Northwest Atlantic Fisheries Centre, St. John's, Newfoundland, unpublished data) in which major prey for the Gulf and 2J3KL inshore regions were Greenland halibut, redfish, Arctic cod, and herring. During the mid-1990s, we modified the proportion of large cod in the hooded seal diet to better reflect the lesser abundance of large cod in the southern Gulf (initial range: 0.5–21.4%, range used: 0.5–17.0%) during the mid-1990s (M. Hammill, unpublished data).

Several studies have examined the diet composition of grey seals in the Gulf of St. Lawrence. These have determined that Atlantic cod, herring, lumpfish (*Cyclopterus lumpus*), wolffish, capelin, mackerel, and ocean pout were the main prey items of this species (Benoit and Bowen 1990; Murie and Lavigne 1992; Proust 1996; Hammill and Stenson 2000). During the mid-1990s, we modified the proportion of large cod in the grey seal diet to better reflect the lesser abundance of large cod in the southern Gulf (initial range: 2.0–23.7%, range used: 2.0–17.0%) during the mid-1990s (M. Hammill, unpublished data).

Harbour seal diet composition was examined in two inshore habitats of Atlantic Canada (lower Bay of Fundy and the north eastern coast of Nova Scotia) between 1988 and 1992 (Bowen and Harrison 1996). For the 250 food-containing stomachs examined, the major prey were Atlantic herring, squid, pollock (*Pollachius virens*), and Atlantic cod.

The upper and lower limits resulting from these different diet studies as well as the modelling estimates for both periods are shown in Table 4.

Table 4. Diet compositions of seals used in modelling for each period. Est: diet estimates by the inverse model; TRN: number of trophic relations; SD: standard deviation. All values are percentages except TRN. Groups with indicated CV (available only as point estimates): Min = mean – (mean x 50%), Max = mean + (mean x 50%). Empty cells indicate that a prey item was never found whereas "0.0" indicates that it was found in very small amounts. Values used in data equations or as upper and lower limit constraints are indicated in boldface.

	Harp seal (mid-1980s)					Harp seal (mid-1990s)				
Prey	Mean	± SD	Min	Max	Est	Mean	± SD	Min	Max	Est
Large cod	1.2	2.7	**0.0**	**3.9**	3.8	1.2	2.7	**0.0**	**1.5**	1.5
Small cod	3.5	7.4	**0.0**	**10.5**	10.4	3.5	7.4	**0.0**	**10.5**	1.0
Green. halibut	3.7	9.4	**0.0**	**13.2**	0.0	3.7	9.4	**0.0**	**13.2**	0.0
Small Amer. plaice	0.7	4.7	**0.0**	**6.6**	6.6	0.7	4.7	**0.0**	**6.6**	5.9
Large Amer. plaice	0.7	4.7	**0.0**	**6.6**	3.2	0.7	4.7	**0.0**	**6.6**	0.0
Flounders	**2.0**	15.7	0.0	22.2	2.0	2.0	15.7	**0.0**	**22.2**	0.4
Skates										
Redfish	2.2	7.4	**0.0**	**10.5**	0.0	2.2	7.4	**0.0**	**10.5**	0.0
Large demersals	**1.0**	7.6	0.0	10.8	1.0	**1.0**	7.6	0.0	10.8	1.0
Small demersals	4.1	3.9	**0.8**	**6.3**	1.1	4.1	3.9	**0.8**	**6.3**	0.8
Capelin	58.5	54.7	**0.0**	**20.0**	13.3	58.5	54.7	**12.4**	**89.8**	75.2
Large pelagics	**0.0**	0.2	0.0	0.2	0.0	**0.0**	0.2	0.0	0.2	0.0
Pisci. small pelagics	2.6	4.4	**0.0**	**6.2**	6.2	2.6	4.4	**0.0**	**6.2**	1.3
Plank. small pelagics	9.9	15.6	**0.0**	**22.0**	21.8	9.9	15.6	**0.0**	**22.0**	3.9
Shrimp	2.8	4.8	**0.0**	**6.8**	5.3	2.8	4.8	**0.0**	**6.8**	2.3
Large crustacea	**0.2**	2.0	0.0	2.8	0.2	**0.2**	2.0	0.0	2.8	0.2
Echinoderms										
Molluscs										
Polychaetes										
Other bent. inver.	**0.2**	2.0	0.0	2.8	0.2	**0.2**	2.0	0.0	2.8	0.2
Large zooplankton	6.6	17.4	**0.0**	**24.7**	24.6	6.6	17.4	**0.0**	**24.7**	6.2
Small zooplankton										
Phytoplankton										
Detritus										
Total	100.0		0.8	176.2	100.0	100.0		13.2	243.7	100.0
TRN	17					17				

Table 4. Cont.

	Hooded seals (mid-1980s)					Hooded seals (mid-1990s)				
Prey	Mean	± SD	Min	Max	Est	Mean	± SD	Min	Max	Est
Large cod	10.6	14.7	**0.5**	**21.4**	20.2	10.6	14.7	**0.5**	**17.0**	17.0
Small cod	10.3	14.3	**0.5**	**20.8**	17.9	10.3	14.3	**0.5**	**20.8**	12.6
Green. halibut	24.5	33.8	**1.3**	**49.2**	1.3	24.5	33.8	**1.3**	**49.2**	1.4
Small Amer. plaice										
Large Amer. plaice										
Flounders	14.8	21.6	**0.0**	**30.6**	22.9	14.8	21.6	**0.0**	**30.6**	29.3
Skates										
Redfish	13.3	12.4	**4.9**	**22.5**	5.0	13.3	12.4	**4.9**	**22.5**	5.5
Large demersals	1.2	1.7	**0.0**	**2.4**	0.7	1.2	1.7	**0.0**	**2.4**	0.2
Small demersals	5.8	8.5	**0.0**	**12.0**	6.0	5.8	8.5	**0.0**	**12.0**	0.0
Capelin	8.9	9.8	**2.2**	**16.1**	11.2	8.9	9.8	**2.2**	**16.1**	13.3
Large pelagics										
Pisci. small pelagics	3.5	5.1	**0.0**	**7.2**	4.9	3.5	5.1	**0.0**	**7.2**	6.4
Plank. small pelagics	7.1	10.4	**0.0**	**14.7**	9.9	7.1	10.4	**0.0**	**14.7**	14.2
Shrimp										
Large crustacea										
Echinoderms										
Molluscs										
Polychaetes										
Other bent. inver.										
Large zooplankton										
Small zooplankton										
Phytoplankton										
Detritus										
Total	100.0		9.4	196.8	100.0	100.0		9.4	192.4	100.0
TRN	10					10				

Table 4. Cont.

	Grey seals (mid-1980s)					Grey seals (mid-1990s)				
Prey	Mean	± SD	Min	Max	Est	Mean	± SD	Min	Max	Est
Large cod	11.7	9.3	**2.0**	**23.7**	23.4	11.7	9.3	**2.0**	**17.0**	17.0
Small cod	11.7	9.3	**1.9**	**23.1**	21.4	11.7	9.3	**1.9**	**23.1**	3.8
Green. halibut	**0.2**	0.4	0.0	0.7	0.2	**0.2**	0.4	0.0	0.7	0.2
Small Amer. plaice	2.9	3.1	**0.0**	**6.2**	5.3	2.9	3.1	**0.0**	**6.2**	6.1
Large Amer. plaice	2.9	3.1	**0.0**	**6.2**	1.7	2.9	3.1	**0.0**	**6.2**	5.0
Flounders	6.5	11.3	**0.0**	**19.6**	17.6	6.5	11.3	**0.0**	**19.6**	19.6
Skates	13.5	23.4	**0.0**	**40.5**	1.9	13.5	23.4	**0.0**	**40.5**	0.7
Redfish										
Large demersals	11.9	8.5	**5.2**	**21.5**	5.7	11.9	8.5	**5.2**	**21.5**	5.3
Small demersals	17.8	11.0	**5.2**	**25.8**	5.9	17.8	11.0	**5.2**	**25.8**	5.2
Capelin	8.7	9.3	**0.6**	**18.8**	2.8	8.7	9.3	**0.6**	**18.8**	18.8
Large pelagics	0.5	0.9	**0.0**	**1.5**	0.2	0.5	0.9	**0.0**	**1.5**	1.3
Pisci. small pelagics	1.3	2.2	**0.0**	**3.8**	3.2	1.3	2.2	**0.0**	**3.8**	3.7
Plank. small pelagics	10.4	3.9	**6.0**	**13.5**	10.6	10.4	3.9	**6.0**	**13.5**	13.3
Shrimp	**0.0**	0.0	0.0	0.0	0.0	**0.0**	0.0	0.0	0.0	0.0
Large crustacea	**0.1**	0.1	0.0	0.2	0.1	**0.1**	0.1	0.0	0.2	0.1
Echinoderms										
Molluscs										
Polychaetes										
Other bent. inver.	**0.0**	0.0	0.0	0.0	0.0	**0.0**	0.0	0.0	0.0	0.0
Large zooplankton	**0.0**	0.0	0.0	0.0	0.0	**0.0**	0.0	0.0	0.0	0.0
Small zooplankton										
Phytoplankton										
Detritus										
Total	100.0		21.0	205.1	100.0	100.0		21.0	198.3	100.0
TRN	17					17				

Table 4. Cont.

Prey	Harbour seals (mid-1980s) (CV= 50%) Mean	± SD	Min	Max	Est	Harbour seals (mid-1990s) (CV= 50%) Mean	± SD	Min	Max	Est
Large cod	1.9		**0.9**	**2.8**	2.3	3.4	2.3	**1.9**	**5.0**	4.8
Small cod	5.6		**2.8**	**8.4**	7.0	4.0	2.3	**2.4**	**5.6**	3.9
Green. halibut										
Small Amer. plaice										
Large Amer. plaice										
Flounders	1.8		**0.9**	**2.7**	2.0	1.8		**0.9**	**2.7**	1.5
Skates	**0.1**		0.1	0.2	0.1	**0.1**		0.1	0.2	0.1
Redfish	**0.4**		0.2	0.6	0.4	**0.4**		0.2	0.6	0.4
Large demersals	2.7		**1.3**	**4.0**	1.7	2.7		**1.3**	**4.0**	1.4
Small demersals	3.0		**1.5**	**4.4**	2.7	3.0		**1.5**	**4.4**	1.5
Capelin	5.9		**2.9**	**8.8**	4.9	5.9		**2.9**	**8.8**	5.8
Large pelagics	8.7		**4.4**	**13.1**	7.1	8.7		**4.4**	**13.1**	. 8.9
Pisci. small pelagics	29.9		**14.9**	**44.8**	28.6	29.9		**14.9**	**44.8**	28.4
Plank. small pelagics	33.5		**16.8**	**50.3**	37.0	33.5		**16.8**	**50.3**	35.9
Shrimp	5.9		**3.0**	**8.9**	5.4	5.9		**3.0**	**8.9**	6.6
Large crustacea	**0.4**		0.2	0.6	0.4	**0.4**		0.2	0.6	0.4
Echinoderms										
Molluscs	**0.2**		0.1	0.3	0.2	**0.2**		0.1	0.3	0.2
Polychaetes										
Other bent. inver.	**0.1**		0.1	0.2	0.1	**0.1**		0.1	0.2	0.1
Large zooplankton										
Small zooplankton										
Phytoplankton										
Detritus										
Total	100.0		50.0	150.0	100.0	100.0		50.5	149.5	100.0
TRN	15					15				

Seabirds

Background

In the Gulf of St. Lawrence, 64.5% of seabirds are estimated to be found inshore while 35.5% are distributed offshore (Cairns et al. 1991). Inshore seabirds breed in a large number of smaller colonies dispersed along the coastline while offshore species breed in a small number of large colonies (Lack 1967). Major inshore species breeding in the region are the great cormorant (*Phalacrocorax carbo*), double-crested cormorant (*Phalacrocorax auritus*), ring-billed gull (*Larus delawarensis*), herring gull (*Larus argentatus*), great black-backed gull (*Larus marinus*),

common tern (*Sterna hirundo*), Arctic tern (*Sterna paradisaea*), and black guillemot (*Cepphus grylle*). Major offshore species that breed in the region are the northern gannet (*Morus bassanus*), black-legged kittiwake (*Rissa tridactyla*), common murre (*Uria aalge*), razorbill (*Alca torda*), Atlantic puffin (*Fratercula arctica*), and Leach's storm-petrel (*Oceanodroma leucorhoa*).

Catch/anthropogenic mortality

There are three primary sources of anthropogenic mortality for seabirds in the region: 1) by-catch in fishing gear, 2) hunting, and 3) oil pollution (Montevecchi and Tuck 1987). A few species of seabirds such as ducks and guillemots are hunted for food in the Gulf of St. Lawrence. Considerable numbers of seabirds (mostly alcids, i.e., murres and puffins, but also others, e.g., gannets) are also caught as by-catch in fishing gear. Bundy et al. (2000) assumed that mortality coming from hunting, by-catch, and maritime traffic amounts to 0.001 t km^{-2} per year. On the basis of information for seabirds from Newfoundland (NAFO divisions 2J3KL) (Bundy et al. 2000), we estimated a catch rate (0.001 t km^{-2} yr^{-1} divided by the seabird biomass, 0.012 t km^{-2}) for the Newfoundland ecosystem and we applied it to the division 4T. It totalled 3.35 x 10^{-4} t km^{-2} yr^{-1} of seabirds being removed annually from the study area through anthropogenic mortality in both periods. The inverse solution estimated catches of 2.76 x 10^{-4} and 3.23 x 10^{-4} t km^{-2} yr^{-1} during the mid-1980s and mid-1990s, respectively.

Biomass

Unlike the open Atlantic coast of Canada, the Gulf of St. Lawrence is not frequented by large numbers of trans-oceanic and trans-equatorial migrants (Brown 1986). Thus, population estimates based on counts of breeding colonies can be used (Cairns et al. 1990). Data on body mass and population estimates for various seabirds were derived from Chapdelaine (Environment Canada, Migratory Birds Division, Sainte-Foy, Québec, unpublished data). In order to estimate biomass density, we assumed that seabirds were distributed uniformly throughout NAFO divisions 4RST. Consequently, biomass was determined by taking the number of birds multiplied by their respective biomass and divided by the whole 4RST bird inventory area (214,000 km^2) instead of the value usually used for the other groups (the sampling area for division 4T). Population surveys typically enumerated the number of breeding pairs. As such, it was necessary to estimate the number of nestling and non-breeding birds. For species that breed within NAFO divisions 4RST, population estimates (Table 5) were calculated as follows (G. Chapdelaine, unpublished data):

Population estimate = breeders
+ nestlings
+ non-breeders (5)

Population estimate (offshore species) = breeding pairs x 2
+ (0.6 x breeding pairs)
+ (0.8 x breeding pairs) (6)

or

Population estimate (inshore species) = breeding pairs x 2
+ (0.6 x breeding pairs)
+ (1.0 x breeding pairs) (7)

The total biomass estimate for the 4T study area is 257 t or 0.004 t km^{-2} for both periods.

Table 5. Approximate period of occupation, population size, average body mass, and biomass for the main species of seabirds that breed within the study area (NAFO division 4T), or breed primarily or completely outside but occur in the study area or are nestlings. Note that the shaded section indicates inshore seabirds while the unshaded section corresponds to offshore seabirds.

Species	Period of occupation	Population (numbers) of breeders	Population (numbers) of non-breeders and nestlings	Individual mass (kg)	Adjusted average biomass (t)
Great cormorant	Apr-Oct	4,968	3,478	2.25	11.085
Double-crested cormorant	Apr-Oct	78,000	54,600	1.67	205.148
Ring-billed gull	Apr-Oct	66,784	53,427	0.50	35.060
Herring gull	Mar-Dec	95,774	76,619	1.12	160.861
Black-headed gull	Apr-Oct	20	16	0.28	0.006
Great black-backed gull	Mar-Dec	19,472	15,578	1.68	49.068
Common tern	May-Sep	52,536	42,029	0.12	4.729
Caspian tern	May-Sep	22	18	0.61	0.010
Arctic tern	May-Sep	2,010	1,608	0.11	0.166
Black guillemot	Jan-Dec	9,524	6,667	0.40	6.477
Leach's storm-petrel	May-Oct	1,036	725	0.05	0.044
Northern gannet	Apr-Oct	84,248	58,974	3.20	267.333
Black-legged kittiwake	Apr-Oct	16,8752	118,126	0.44	73.628
Common murre	May-Sep	89,320	62,524	0.99	87.685
Thick-billed murre	Apr-Oct	24	17	0.93	0.022
Razorbill	Apr-Oct	16,500	11,550	0.72	11.781
Atlantic puffin	Apr-Oct	48,348	33,844	0.46	22.054
TOTAL	Jan-Dec	651,141	539,790	-	859.176

Production

An energetics model developed for seabirds of the whole Gulf of St. Lawrence (4RST) (G. Chapdelaine, unpublished data) indicates that there is a total of 221,201 nestlings produced each year for all species combined (calculated by assuming that nestlings = number of breeding pairs x 0.6). Multiplying the number of nestlings by the average mass for each species results in a total annual production of 0.0011 t km^{-2} yr^{-1} for the two periods. The inverse solution estimated a production of 0.0011 (P/B = 0.267 yr^{-1}) and 0.0011 t km^{-2} yr^{-1} (P/B = 0.264 yr^{-1}) during the mid-1980s and mid-1990s, respectively.

Consumption

Estimated food consumption for seabirds in the Gulf is 108,419 t yr^{-1} (Chapdelaine, unpublished data). Assuming that consumption is evenly distributed throughout the region results in an estimated annual consumption of 0.507 t km^{-2} yr^{-1} for both periods.

Based on the previous annual production and the upper GE limit (1%; the value based on the lower GE limit of 0.1% was not realistic), we obtained another consumption estimate of 0.111 t km^{-2} yr^{-1} for each period. This resulted in a mean consumption of 0.309 ± 0.280 t km^{-2} yr^{-1} for each period. The inverse solution estimated a consumption of 0.177 t km^{-2} yr^{-1}, representing a Q/B of 44.185 yr^{-1} during the mid-1980s. During the mid-1990s, the modelling estimate was 0.131 t km^{-2} yr^{-1} (Q/B = 32.747 yr^{-1}).

Diet composition

Seabirds within the study area feed at a variety of trophic levels with most prey being small pelagic fish, benthic invertebrates, and pelagic crustaceans (Cairns et al. 1990). Great cormorants feed mostly on benthic fish, primarily flatfish and cunners (*Tautogolabrus adspersus*), while double-crested cormorants prey heavily on flatfish, sculpins (*Myoxocephalus* sp.), rock gunnels (*Pholis gunnellus*), and sand lance (*Ammodytes americanus*). The only data available from the Gulf of St. Lawrence for black guillemot showed that chicks are fed primarily with benthic fish, particularly sculpins, blennies, and tomcod (*Microgadus tomcod*) (Cairns 1981). Northern gannet, the largest breeding seabird species in the study area, preys on large pelagic species such as mackerel and Atlantic saury (*Scomberesox saurus*), but also on sand lance (Burton 1980). Herring gulls, which are the most abundant species in the study area, feed primarily on small pelagic fish and non-marine food (Threlfall 1968; Haycock and Threlfall 1975; Pierroti 1983), but quantitative dietary data from the Gulf are generally lacking for this species as well as for all other gulls, terns, storm-petrels, kittiwakes, and offshore alcids (Cairns et al. 1990). The diets of Arctic tern, recorded on Québec's North Shore (NAFO division 4S; Chapdelaine et al. 1985), as well as the diet of the common tern, the most abundant species in the eastern part of the area (NAFO division 4R), consisted mainly of capelin, sand lance, and pelagic invertebrates. Black-legged kittiwakes feed primarily on copepods and euphausiids (Threlfall 1968; Maunder and Threlfall 1972). The final seabird diet was modified following Cairns et al. (1990) and Chapdelaine (unpublished data), who used all available information for the Gulf of St. Lawrence

as well as extrapolated information from the closest ecosystems to create a complete diet for all seabird species found in the Gulf of St. Lawrence (north and south, NAFO divisions 4RST). There is no diet data available for Leach's storm-petrel, kittiwakes, murres, razorbills, or Atlantic puffins from the Gulf. Information for these species has been extrapolated from Labrador, eastern Newfoundland, and Nova Scotia (Bundy et al. 2000). Based on these different studies, we estimated the resulting diet composition of seabirds used in modelling for the southern Gulf of St. Lawrence in each period (Table 6).

Table 6. Diet composition of seabirds used in modelling for each period. Est: diet estimates by the inverse model; TRN: number of trophic relations; SD: standard deviation. All values are percentages except TRN. Empty cells indicate that a prey item was never found whereas "0.0" indicates that it was found in very small amounts. Values used in data equations or as upper and lower limit constraints are indicated in boldface.

	Seabirds					
Prey	Mean	± SD	Min	Max	Est. (mid-1980s)	Est. (mid-1990s)
Large cod						
Small cod	**0.2**	0.3	0.0	0.5	0.2	0.1
Green. halibut	**0.5**	0.4	0.0	0.8	0.5	0.7
Small Amer. plaice	**0.5**	0.4	0.0	0.8	0.5	0.7
Large Amer. plaice	**0.0**	0.0	0.0	0.0	0.0	0.0
Flounders	**0.5**	0.4	0.0	0.8	0.5	0.7
Skates	**0.5**	0.4	0.0	0.8	0.5	0.7
Redfish						
Large demersals						
Small demersals	7.7	8.1	**1.6**	**16.9**	1.6	4.7
Capelin	46.0	27.5	**21.9**	**76.0**	37.5	31.7
Large pelagics	**0.0**	0.1	0.0	0.1	0.0	0.0
Pisci. small pelagics	7.8	11.9	**0.2**	**21.5**	13.9	15.5
Plank. small pelagics	31.3	25.5	**7.9**	**58.4**	35.8	43.3
Shrimp	0.7	0.7	**0.0**	**1.4**	0.3	0.9
Large crustacea						
Echinoderms						
Molluscs	**0.0**	0.1	0.0	0.1	0.0	0.0
Polychaetes						
Other bent. inver.	0.5	0.8	**0.0**	**1.4**	0.9	1.1
Large zooplankton	3.7	6.4	**0.0**	**11.1**	7.6	0.0
Small zooplankton	**0.2**	0.3	0.0	0.5	0.2	0.0
Phytoplankton						
Detritus						
Total	100.0		31.6	191.2	100.0	100.0
TRN	16					

Atlantic cod

Background

The southern Gulf cod stock concentrates in winter in the deep waters off Cape Breton in NAFO fishing divisions 4Vn and northern 4Vs and usually begins the return migration to the Gulf in mid-April. Spawning takes place mainly in the Shediac Valley and around the Îles-de-la-Madeleine from late April to early July (DFO 2002a). During summer, the population is widely distributed in 4T.

Commercial catches increased from the 1940s and reached a peak in 1958. Landings remained relatively high until the stock declined to low levels in the mid-1970s. The stock recovered during the 1980s before it collapsed in the 1990s.

For the purpose of this study, Atlantic cod were divided into adults and juveniles, or more precisely, into large and small fish. Smaller fish prey mainly on invertebrates while larger fish feed mainly on fish. These changes tend to occur gradually with increasing length, but here it was assumed that the change occurs at 35 cm for cod (Lilly 1991). Southern Gulf cod of age 4+ generally represent fish ≥ 35 cm of length, at which size cod become more piscivorous and begin to be recruited to the commercial fishery.

Catch

Catch data for cod age 4+ (minimum commercial size: 43 cm) in NAFO division 4T are available in Chouinard et al. (1999). The 1994–1996 period modelled here corresponds to the first moratorium on cod fishing in the area. There was no directed cod fishery during these years. The average landings were 62,416 and 1,172 t during the mid-1980s and mid-1990s, respectively, corresponding to mean catches of $9.72 \times 10^{-1} \pm 1.11 \times 10^{-1}$ and $1.80 \times 10^{-2} \pm 2.39 \times 10^{-3}$ t km^{-2} yr^{-1}. In the absence of information on misreported catches for this species, we decided to use the upper catch limit (1.07 t km^{-2} yr^{-1}) to constrain the mid-1980 model and the upper catch limit increasing by 50% (3.10×10^{-2} t km^{-2} yr^{-1}) to constrain the mid-1990 model after different preliminary tests. Since it was assumed that small cod are not recruited to the fishery, and information on by-catch was not available for the southern Gulf area, catch in the model was set to zero for this group. The modelling estimates for large cod were 1.10 and 3.05×10^{-2} t km^{-2} yr^{-1} during the mid-1980s and mid-1990s, respectively.

Biomass

Annual biomass estimates were based on catches in a bottom-trawl survey conducted in the southern Gulf each September. These survey estimates were converted to estimates of total biomass using the catchability coefficients reported in Table 2. Total biomass was estimated each year by multiplying the abundance estimate for each length increment by mean weight at length (derived from length–weight relationships) and summing the results. This resulted in mean biomass estimates of large cod of 336,295 t or 5.248 t km^{-2} (SD = 0.956 t km^{-2}) during the mid-

1980s and 103,095 t or 1.609 t km^{-2} (SD = 0.237 t km^{-2}) during the mid-1990s. For small cod (< 35 cm), the mean biomass estimates were 79,932 t or 1.247 t km^{-2} (SD = 0.322 t km^{-2}) during the mid-1980s and 19,151 t or 0.299 t km^{-2} (SD = 0.017 t km^{-2}) during the mid-1990s.

Production

The production of large cod was estimated by catch-curve analysis of groundfish survey data from NAFO division 4T. The estimate of total mortality (Z) was determined from the slope of the regression line fitted to the downward side of the catch curve (Sinclair 2001). This resulted in a Z estimate of 0.77 (with a 95% CI of 0.62 to 0.92) for the 1985–1987 period and 0.44 (with a 95% CI of 0.31 to 0.57) for the 1994–1996 period. We used the equation ($A = 1 - e^{-Z}$) (Ricker 1980) to convert the instantaneous mortality rate Z to total annual mortality A (yr^{-1}). Thus, annual mortality rates ranged between 0.46 and 0.60 yr^{-1} and between 0.27 and 0.43 yr^{-1} during the mid-1980s and mid-1990s, respectively. Since we assume a steady state (no year-to-year change in biomass), annual mortality rate A (converted to biomass) is equal to the P/B ratio (Allen 1971). By multiplying the A ranges by the mean biomass for each period, we obtained annual production estimates of 2.817 ± 0.514 t km^{-2} yr^{-1} (range: 2.427–3.153 t km^{-2} yr^{-1}) and 0.573 ± 0.191 t km^{-2} yr^{-1} (range: 0.429–0.699 t km^{-2} yr^{-1}) during the mid-1980s and mid-1990s, respectively. The inverse solution estimated a production of 2.434 t km^{-2} yr^{-1}, representing a P/B (= A) of 0.464 yr^{-1} during the mid-1980s. During the mid-1990s, the modelling estimate was 0.429 t km^{-2} yr^{-1}, representing a P/B (= A) of 0.267 yr^{-1}.

For small cod, production was assumed to be equivalent to biomass multiplied by natural mortality (M), plus catch ([B x M] + C). Natural mortality for small cod was assumed to be 0.6 yr^{-1}, while there were no catch estimates of small cod (D. Swain, pers. comm.). Using the minimum and maximum biomass values for small cod, we estimated a production range between 0.452 and 0.967 t km^{-2} yr^{-1}, corresponding to an annual production of 0.656 ± 0.241 t km^{-2} yr^{-1} during the mid-1980s. During the mid-1990s, the production range was from 0.127 to 0.189 t km^{-2} yr^{-1}, corresponding to an annual production of 0.157 ± 0.013 t km^{-2} yr^{-1}. The inverse solution estimated a production of 0.779 t km^{-2} yr^{-1} (P/B = 0.624 yr^{-1}) and 0.171 t km^{-2} yr^{-1} (P/B = 0.572 yr^{-1}) during the mid-1980s and mid-1990s, respectively.

Consumption

Q/B estimates were extrapolated from food intake measurements (daily or yearly consumption) and body mass or biomass of fish under study. This approach yielded an estimated Q/B ratio of 1.96 yr^{-1} for large cod in the southern Gulf using data from Waiwood et al. (1980). Multiplying this Q/B ratio by the minimum and maximum biomass values for each period, this resulted in consumption ranges of 8.153 to 11.597 t km^{-2} yr^{-1} and 2.747 to 3.664 t km^{-2} yr^{-1} during the mid-1980s and mid-1990s, respectively. Based on the previous mean production for large cod for each period (2.817 and 0.573 t km^{-2} yr^{-1}) and the minimum and maximum GE limits (10–30%), we obtained other consumption values of 9.390 to 28.171 t km^{-2} yr^{-1} and 1.909 to 5.727 t km^{-2} yr^{-1} during the mid-1980s and mid-1990s, respectively. The resulting lower and upper consumption limits were thus 8.153 and 28.171 t km^{-2} yr^{-1} during the mid-1980s and 1.909 and

5.727 t km^{-2} yr^{-1} during the mid-1990s. The inverse solution estimated a consumption of 8.231 t km^{-2} yr^{-1} (Q/B of 1.568 yr^{-1}) and 3.512 t km^{-2} yr^{-1} (Q/B of 2.183 yr^{-1}) during the mid-1980s and mid-1990s, respectively.

For small cod, we obtained a Q/B ratio of 3.25 yr^{-1} from Waiwood et al. (1980). Multiplying this Q/B ratio by the minimum and maximum biomass values for each period resulted in consumption ranges of 3.258 to 5.238 t km^{-2} yr^{-1} and 0.912 to 1.023 t km^{-2} yr^{-1} during the mid-1980s and mid-1990s, respectively. Based on the previous mean production for small cod for each period (0.656 and 0.157 t km^{-2} yr^{-1}) and the minimum and maximum GE limits (10–30%), we obtained other consumption values of 2.186 to 6.557 t km^{-2} yr^{-1} and 0.524 to 1.571 t km^{-2} yr^{-1} during the mid-1980s and mid-1990s, respectively. The resulting lower and upper consumption limits were thus 2.186 and 6.557 t km^{-2} yr^{-1} during the mid-1980s and 0.524 and 1.571 t km^{-2} yr^{-1} during the mid-1990s. The inverse solution estimated a consumption of 3.884 t km^{-2} yr^{-1} (Q/B of 3.113 yr^{-1}) and 1.165 t km^{-2} yr^{-1} (Q/B of 3.896 yr^{-1}) during the mid-1980s and mid-1990s, respectively.

Diet composition

Stomach content data were available from NAFO division 4T (Hanson and Chouinard 2002; M. Hanson, unpublished data). Sampling was length-stratified and covered each season. For the 1985–1987 period, we used samples from 1987 (n = 1,288 and 181 stomachs for large and small cod, respectively). Overall, on average the most important prey items of large cod, in percent mass of stomach content, were large zooplankton, molluscs, large crustaceans, and polychaetes (57.9% of the diet; Table 7). The most important prey items of small cod were large zooplankton, other benthic invertebrates, and shrimp (81.7%; Table 7).

For the 1994–1996 period, we used samples from 1990–1999 (n = 6,691 and 2,501 stomachs for large and small cod, respectively). Overall, the most important prey items of large cod, in percent mass of stomach content, were shrimp, planktivorous small pelagics, and large zooplankton (49.3% of the diet; Table 7). The most important prey items of small cod were large zooplankton, shrimp, and other benthic invertebrates (75.5%; Table 7).

Table 7. Diet compositions of large and small cod used in modelling for each period. Est: diet estimates by the inverse model; TRN: number of trophic relations; SD: standard deviation. All values are percentages except TRN. Empty cells indicate that a prey item was never found whereas "0.0" indicates that it was found in very small amounts. Values used in data equations or as upper and lower limit constraints are indicated in boldface.

	Large cod (mid-1980s)					Large cod (mid-1990s)				
Prey	Mean	± SD	Min	Max	Est	Mean	± SD	Min	Max	Est
Large cod										
Small cod	**3.1**	16.0	1.0	23.6	3.1	4.9	4.2	**2.0**	**8.0**	2.0
Green. halibut										
Small Amer. plaice	0.5	2.1	**0.0**	**2.9**	2.9	1.8	17.1	**0.0**	**24.2**	22.7
Large Amer. plaice										
Flounders	0.8	2.6	**0.0**	**3.7**	0.3	1.1	17.0	**0.0**	**24.1**	1.5
Skates										
Redfish										
Large demersals										
Small demersals	4.8	8.0	**1.9**	**13.2**	1.9	6.2	23.7	**0.0**	**33.6**	0.0
Capelin	2.0	3.6	**1.0**	**6.1**	1.1	**5.5**	28.6	0.0	40.5	5.6
Large pelagics										
Pisci. small pelagics	2.0	3.6	**1.0**	**6.1**	6.1	1.5	2.1	**0.0**	**3.0**	0.8
Plank. small pelagics	**8.9**	22.1	1.0	32.3	8.9	16.6	63.2	**0.0**	**89.3**	9.9
Shrimp	**6.9**	10.9	0.2	15.5	6.9	18.2	70.7	**0.0**	**100.0**	7.3
Large crustacea	12.2	18.1	**3.1**	**28.7**	3.1	6.0	23.0	**0.0**	**32.5**	0.6
Echinoderms	**2.3**	8.9	0.0	12.5	2.3	**1.9**	25.6	0.0	36.3	2.0
Molluscs	**13.4**	17.0	1.0	25.0	13.4	10.2	36.6	**0.0**	**51.8**	18.2
Polychaetes	11.4	11.9	**0.6**	**17.4**	12.8	7.5	30.5	**0.0**	**43.1**	14.0
Other bent. inver.	10.4	12.7	**0.1**	**18.0**	14.4	**3.9**	17.9	0.0	25.3	4.0
Large zooplankton	20.9	21.1	**0.1**	**29.9**	22.5	14.5	50.1	**0.0**	**70.8**	11.1
Small zooplankton	**0.3**	0.3	0.0	0.4	0.3	**0.2**	1.5	0.0	2.1	0.2
Phytoplankton										
Detritus										
Total	100.0		10.8	235.4	100.0	100.0		2.0	584.6	100.0
TRN	15					15				

Table 7. Cont.

Prey	Small cod (mid-1980s)					Small cod (mid-1990s)				
	Mean	± SD	Min	Max	Est	Mean	± SD	Min	Max	Est
Large cod										
Small cod	**0.0**	0.0	0.0	0.0	0.0	**0.9**	8.7	0.0	12.3	0.9
Green. halibut										
Small Amer. plaice	**0.0**	0.0	0.0	0.0	0.0	0.1	2.0	**0.0**	**2.8**	2.5
Large Amer. plaice										
Flounders	4.9	11.8	**0.0**	**16.8**	1.1	0.2	4.0	**0.0**	**5.7**	1.9
Skates										
Redfish										
Large demersals										
Small demersals	3.2	1.5	**0.0**	**2.1**	0.0	2.7	10.2	**0.0**	**14.4**	0.0
Capelin	**0.0**	0.0	0.0	0.0	0.0	**2.1**	10.8	0.0	15.3	2.1
Large pelagics										
Pisci. small pelagics	**0.0**	0.0	0.0	0.0	0.0	**0.0**	0.0	0.0	0.0	0.0
Plank. small pelagics	**0.0**	0.0	0.0	0.0	0.0	**3.9**	45.0	0.0	63.7	3.9
Shrimp	6.8	9.0	**2.7**	**15.4**	5.0	28.2	62.5	**0.0**	**88.4**	21.5
Large crustacea	1.6	5.8	**0.3**	**8.5**	0.4	**2.1**	19.9	0.0	28.1	2.1
Echinoderms	**0.1**	2.1	0.0	3.0	0.1	**0.2**	1.1	0.0	1.5	0.2
Molluscs	1.6	1.3	**0.0**	**1.8**	1.5	1.6	6.4	**0.0**	**9.0**	5.2
Polychaetes	6.1	5.2	**0.0**	**7.4**	7.1	8.4	29.9	**0.0**	**42.2**	17.9
Other bent. inver.	13.2	7.7	**9.7**	**20.6**	17.0	**11.3**	45.5	0.0	64.3	11.3
Large zooplankton	61.7	14.6	**49.0**	**69.6**	65.2	36.1	63.8	**0.9**	**91.0**	28.3
Small zooplankton	0.8	1.9	**0.0**	**2.7**	2.7	**2.3**	26.6	0.0	37.6	2.3
Phytoplankton										
Detritus										
Total	100.0		61.6	147.8	100.0	100.0		0.9	476.5	100.0
TRN	15					15				

Greenland halibut

Background

Greenland halibut (*Reinhardtius hippoglossoides*) is a deep-water flatfish present in the North Atlantic and North Pacific. In the northwest Atlantic, they are found from Arctic regions to Georges Bank (Bowering 1983). The Gulf of St. Lawrence population is considered to be a small stock, isolated from the main northwest Atlantic stock, completing its entire life cycle within the Gulf (DFO 2002b).

Directed fishing for this species with bottom trawls and gillnets developed after the mid-1970s. Catches increased in the 1980s to reach an all-time high in 1987 (11,000 t) but have since declined to around 3,000 t (DFO 2002b).

Catch

According to NAFO fisheries statistics, the mean annual landings of Greenland halibut in 4T was 4,009 and 1,694 t during the mid-1980s and mid-1990s, respectively (NAFO 1999). Since the study area covered only a fraction of 4T, we used the ratio of the biomass estimated in the study area (biomass in survey strata 416-438 excluding stratum 425) to the whole 4T biomass (biomass in all survey strata) for each period as a correction factor for catch. The correction factors for catch were 0.13 and 0.07, respectively, for the two periods. This resulted in a mean annual catch of $7.13 \times 10^{-3} \pm 3.42 \times 10^{-3}$ and $1.92 \times 10^{-3} \pm 1.13 \times 10^{-3}$ t km^{-2} yr^{-1} during the mid-1980s and mid-1990s, respectively. The inverse solution estimated a catch of 3.28×10^{-3} and 1.91×10^{-3} t km^{-2} yr^{-1}, respectively, for the two periods.

Biomass

Annual biomass estimates were obtained from the groundfish survey in the NAFO division 4T each September. The length-frequency data were corrected for catchability. Total biomass was estimated each year by multiplying the abundance estimate for each length increment by mean weight-at-length (derived from length–weight relationships) and summing the results. This resulted in mean biomass estimates of 591 t or 0.009 t km^{-2} (SD = 0.004 t km^{-2}) and 451 t or 0.007 t km^{-2} (SD = 0.001 t km^{-2}) during the mid-1980s and mid-1990s, respectively.

Production

Due to the lack of reliable information on production (P) and total mortality (Z) of this species, it was assumed that production was equivalent to biomass multiplied by natural mortality (M), plus catch (Allen 1971). Natural mortality for Greenland halibut (M = 0.09 yr^{-1}) was estimated using FishBase (Froese and Pauly 2002) and a maximal length of 96.5 cm along with a water temperature of 3°C. When the minimum and maximum biomass values were used for each

period, we obtained a production range of 0.004 to 0.011 and 0.001 to 0.008 t km^{-2} yr^{-1}, respectively, for the two periods. The modelling estimates were 0.009 t km^{-2} yr^{-1} (P/B = 0.956 yr^{-1}) and 0.008 t km^{-2} yr^{-1} (P/B = 1.119 yr^{-1}) during the mid-1980s and mid-1990s, respectively.

Consumption

Four Q/B ratios for Greenland halibut were obtained from three different sources. Two Q/B values were estimated using daily food requirements of 5-year-old (4.427 yr^{-1}) and 6- to 20-year-old Greenland halibut (1.660 yr^{-1}) from the northwest Atlantic (Chumakov and Podrazhanskaya 1986). Another Q/B ratio (1.500 yr^{-1}) was calculated using FishBase (Froese and Pauly 2002) for fish at 2°C and having a maximum mass of 586 g. A fourth Q/B estimate was obtained from a feeding study conducted in West Greenland (Pedersen and Riget 1992a). In that study, a total of 3,030 stomachs was analyzed and the average daily ration of fish (average of autumn–winter and spring–summer estimates) was 0.73 % body mass per day. This resulted in a Q/B ratio of 2.665 yr^{-1}. When the minimum and maximum biomass values were used for each period and based on these four previous Q/B ratios, this resulted in a consumption range of 0.010 to 0.059 and 0.009 to 0.034 t km^{-2} yr^{-1}, respectively, for the two periods.

Based on the mean production (0.008 and 0.005 t km^{-2} yr^{-1}) for each period and the minimum and maximum GE limits (10–30%), we obtained other consumption ranges of 0.026 to 0.079 and 0.016 to 0.049 t km^{-2} yr^{-1} during the mid-1980s and mid-1990s, respectively. The resulting lower and upper consumption limits were thus 0.010 to 0.079 t km^{-2} yr^{-1} and 0.009 to 0.049 t km^{-2} yr^{-1}, respectively, for the two periods. The inverse solution estimated a consumption of 0.042 t km^{-2} yr^{-1} (Q/B = 4.510 yr^{-1}) and 0.035 t km^{-2} yr^{-1} (Q/B = 5.030 yr^{-1}) during the mid-1980s and mid-1990s, respectively.

Diet composition

Stomach content data for Greenland halibut from NAFO division 4T were not available for the studied periods. Diet information for this group was taken from the northern Gulf (Morisette et al. 2003; Savenkoff et al. 2004). In the northern Gulf, Greenland halibut were divided into fish larger or smaller than 40 cm and diet data were collected from 1993 to 2002. The diet compositions of small and large Greenland halibut were weighted by the biomass of each group during the mid-1980s (51% and 49% of small and large Greenland halibut, respectively) and the mid-1990s (57% and 43% of small and large Greenland halibut, respectively). The most important prey items of Greenland halibut were capelin, shrimp, and large zooplankton (77.4 and 79.2% of the diets for the two periods; Table 8).

Table 8. Diet composition of Greenland halibut used in modelling for each period. Est: diet estimates by the inverse model; TRN: number of trophic relations; SD: standard deviation. All values are percentages except TRN. Empty cells indicate that a prey item was never found whereas "0.0" indicates that it was found in very small amounts. Values used in data equations or as upper and lower limit constraints are indicated in boldface.

	Greenland halibut (mid-1980s)					Greenland halibut (mid-1990s)				
Prey	Mean	± SD	Min	Max	Est	Mean	± SD	Min	Max	Est
Large cod										
Small cod	**0.0**	0.0	0.0	0.0	0.0	**0.0**	0.0	0.0	0.0	0.0
Green. halibut	**0.1**	0.1	0.0	0.2	0.1	**0.1**	0.1	0.0	0.1	0.1
Small Amer. plaice	**0.1**	0.1	0.0	0.2	0.1	**0.1**	0.1	0.0	0.1	0.1
Large Amer. plaice										
Flounders	**0.1**	0.1	0.0	0.2	0.1	**0.1**	0.1	0.0	0.1	0.1
Skates	**0.0**	0.0	0.0	0.0	0.0	**0.0**	0.0	0.0	0.0	0.0
Redfish	3.9	5.0	**0.4**	**7.5**	0.4	3.5	4.5	**0.3**	**6.6**	0.9
Large demersals										
Small demersals	9.8	10.8	**2.2**	**17.5**	6.8	9.5	10.4	**2.1**	**16.8**	2.1
Capelin	50.3	22.6	**34.4**	**66.3**	53.3	51.7	24.4	**34.4**	**69.0**	55.2
Large pelagics	**0.0**	0.0	0.0	0.0	0.0	**0.0**	0.0	0.0	0.0	0.0
Pisci. small pelagics	0.9	0.9	**0.3**	**1.5**	0.8	1.0	0.9	**0.3**	**1.6**	1.1
Plank. small pelagics	7.5	6.2	**3.1**	**11.9**	8.5	6.6	5.5	**2.7**	**10.5**	6.9
Shrimp	15.8	5.5	**12.0**	**19.7**	15.0	15.2	5.9	**11.0**	**19.4**	15.9
Large crustacea	**0.0**	0.0	0.0	0.0	0.0	**0.0**	0.0	0.0	0.0	0.0
Echinoderms	**0.0**	0.0	0.0	0.0	0.0	**0.0**	0.0	0.0	0.0	0.0
Molluscs	**0.0**	0.0	0.0	0.0	0.0	**0.0**	0.0	0.0	0.0	0.0
Polychaetes	**0.0**	0.0	0.0	0.0	0.0	**0.0**	0.0	0.0	0.0	0.0
Other bent. inver.	**0.0**	0.0	0.0	0.1	0.0	**0.0**	0.0	0.0	0.1	0.0
Large zooplankton	11.3	13.0	**2.1**	**20.5**	14.8	12.2	14.1	**2.3**	**22.2**	17.4
Small zooplankton	**0.0**	0.0	0.0	0.0	0.0	**0.0**	0.0	0.0	0.0	0.0
Phytoplankton										
Detritus										
Total	100.0		54.5	145.5	100.0	100.0		53.3	146.7	100.0
TRN	19					19				

American plaice, flounders, and skates

Background

The remaining flatfish were divided into four groups: small and large American plaice (*Hippoglossoides platessoides*), flounders, and skates.

American plaice is widely distributed throughout the northwest Atlantic (from west Greenland to the Gulf of Maine) and is usually found at intermediate depths (80–250 m) (Morin et al. 1998). American plaice were separated into two groups (< 35 cm and ≥ 35 cm) based on diet, age/size at first capture in fisheries, and age/size at maturity (Pitt 1973). In 4T, landings ranged between 6000 and 12,000 t from 1965 to the late 1980s, and dropped sharply in 1993 in response to closure of the cod fishery and restrictive management measures. Since 1996, landings have been below 2000 t.

The flounder group consisted of witch flounder (*Glyptocephalus cynoglossus*), yellowtail flounder (*Limanda ferruginea*), winter flounder (*Pseudopleuronectes americanus*), and windowpane (*Scophthalmus aquosus*). Flounder were grouped together on the basis of their similar feeding behaviour. These four species are bottom-dwelling flatfish that live in relatively shallow water, except for witch flounder, which lives mostly in deeper waters. Their distribution ranges from the coast of Labrador in the north to North Carolina in the south. Witch flounder, yellowtail flounder, and winter flounder are of commercial importance in 4T. Since the 1950s, important commercial landings of witch flounder have been made in the deep waters bordering the Laurentian Channel. A long-standing fishery has also been in place in shallower waters for winter flounder.

The skate group included three species: the thorny skate (*Amblyraja radiata*), considered here as the key species for the group due to its higher relative abundance and broader distribution within the southern Gulf, the winter skate (*Leucoraja ocellata*), and the smooth skate (*Malacoraja senta*). The thorny skate is widely distributed throughout the North Atlantic. The greatest concentrations are generally found in the deeper part of continental shelves, at depths greater than 110 m (McEachran et al. 1976). Winter skate are distributed from Georges Bank north into the Gulf of St. Lawrence and are also found south of Newfoundland. It has been reported from less than 1 m in depth (Bigelow and Schroeder 1953) to 371 m by Scott and Scott (1988). During the summer in 4T, winter skates concentrate in the near-shore areas of Prince Edward Island and New Brunswick and east of the Îles-de-la-Madeleine (Simon et al. 2003). The smooth skate is found throughout the northwest Atlantic, from the Gulf of St. Lawrence to Georges Bank (Scott and Scott 1988). Surveys conducted since the 1940s have shown that the greatest concentrations are found in the Gulf of St. Lawrence, on the Grand Banks, and on the Scotian Shelf. This species lives at depths of 50 to 700 m but is mostly caught between 90 and 325 m (McKone and LeGrow 1983). There is no directed fishery for skates in the southern Gulf. They are however captured as by-catch in other commercial fisheries.

Catch

According to landing statistics (NAFO 1999), the mean annual landings of large American plaice in NAFO division 4T were 8,320 and 2,073 t during the 1985–1987 and 1994–1996

periods, respectively. Since the study area covered only a fraction of 4T, we used the ratio of the biomass estimated in the study area (biomass in survey strata 416-438 excluding stratum 425) to the whole 4T biomass (biomass in all survey strata) for each period as a correction factor for catch. The correction factors for catch were 1.00 and 0.99, respectively, for the two periods. This resulted in a mean annual catch of $1.30 \times 10^{-1} \pm 1.66 \times 10^{-2}$ and $3.22 \times 10^{-2} \pm 9.07 \times 10^{-3}$ t km^{-2} yr^{-1} during the mid-1980s and mid-1990s, respectively. The inverse solution estimated a catch of 1.31×10^{-1} and 3.42×10^{-2} t km^{-2} yr^{-1}, respectively, for the two periods.

Landings were assumed to be negligible for small American plaice. This was not a good assumption because the legal size is 30 cm. Approximately, 30% and 50% (by number) of the landings were plaice < 35 cm in 1985–1987 and 1994–1996, respectively (D. Swain, unpublished data). However, a large part of the total mortality of small American plaice (39 and 28% during the mid-1980s and mid-1990s, respectively) was unexplained in the two models. A large part of this unexplained mortality could be related to unaccounted or unreported landings. Indeed, the American plaice fishery in the southern Gulf has involved a considerable amount of discard of fish below market size during some periods such as the 1980s (Tallman 1991 and references therein).

The landings of flounders were calculated by summing NAFO landing statistics for each of the species listed above (NAFO 1999). For winter flounder, the mean annual landings in 4T were 1,678 and 891 t during the 1985–1987 and 1994–1996 periods, respectively. The area correction factor estimated by the biomass ratio between the study area and 4T was 1 for each period. For witch flounder, the mean annual landings in 4T were 1,255 and 346 t during the 1985–1987 and 1994–1996 periods, respectively. The area correction factor was 0.77 and 0.84, respectively, for the two periods. For yellowtail flounder, the mean annual landings in 4T were 338 and 158 t during the 1985–1987 and 1994–1996 periods, respectively. The area correction factor was 1 for each period. The resulting annual catch of flounders was $4.62 \times 10^{-2} \pm 1.02 \times 10^{-2}$ and $2.09 \times 10^{-2} \pm 3.68 \times 10^{-3}$ t km^{-2} yr^{-1} in the mid-1980s and mid-1990s, respectively. The modelling catch estimate was 4.55×10^{-2} and 2.10×10^{-2} t km^{-2} yr^{-1}, respectively, for the two periods.

Finally, the mean annual landings of skates in 4T were 1 and 38 t during the 1985–1987 and 1994–1996 periods, respectively (NAFO 1999). Estimates of by-catch fishing mortality were not available at the time this report was written, but may have been important. The area correction factor was 0.93 and 0.69, respectively, for the two periods. The resulting annual catch of skates was $1.43 \times 10^{-5} \pm 2.48 \times 10^{-5}$ and $4.19 \times 10^{-4} \pm 2.09 \times 10^{-4}$ t km^{-2} yr^{-1} in the mid-1980s and mid-1990s, respectively. The modelling catch estimate was 1.81×10^{-5} and 3.80×10^{-4} t km^{-2} yr^{-1}, respectively, for the two periods.

Biomass

Annual biomass estimates were obtained from the groundfish survey in the NAFO division 4T each September. The length-frequency data were corrected for catchability. Total biomass was estimated each year by multiplying the abundance estimate for each length increment by mean weight at length (derived from length–weight relationships) and summing the results. During the mid-1980s, this resulted in mean biomass estimates of 307,703 t or 4.802 t km^{-2} (SD = 0.836 t km^{-2}) for small American plaice, 35,200 t or 0.549 t km^{-2} (SD = 0.099 t km^{-2}) for large American plaice, 100,028 t or 1.561 t km^{-2} (SD = 0.447 t km^{-2}) for flounders, and 5,107 t or 0.080 t km^{-2}

(SD = 0.013 t km^{-2}) for skates. Mean biomass during the mid-1990s was estimated at 244,466 t or 3.815 t km^{-2} (SD = 0.606 t km^{-2}) for small American plaice, 16,753 t or 0.261 t km^{-2} (SD = 0.032 t km^{-2}) for large American plaice, 106,177 t or 1.657 t km^{-2} (SD = 0.407 t km^{-2}) for flounders, and 2,538 t or 0.040 t km^{-2} (SD = 0.006 t km^{-2}) for skates.

Production

It was assumed that for each group, production is equivalent to biomass multiplied by natural mortality (M), plus the catch (Allen 1971). Natural mortality was assumed to be 0.440 yr^{-1} for small American plaice, 0.220 yr^{-1} for large American plaice (Pitt, 1982), and 0.214 yr^{-1} for skates (Simon and Frank 1996). Due to a lack of information, natural mortality of flounders was simply assumed to be 0.200 yr^{-1}. When the minimum and maximum biomass values were used for each group, we obtained production ranges of 1.370 to 2.383 t km^{-2} yr^{-1} for small American plaice, 0.212 to 0.277 t km^{-2} yr^{-1} for large American plaice, 0.274 to 0.465 t km^{-2} yr^{-1} for flounders, and 0.014 to 0.020 t km^{-2} yr^{-1} for skates during the mid-1980s. During the mid-1990s, the production ranges were 1.195 to 1.981 t km^{-2} yr^{-1} for small American plaice, 0.080 to 0.095 t km^{-2} yr^{-1} for large American plaice, 0.268 to 0.440 t km^{-2} yr^{-1} for flounders, and 0.007 to 0.010 t km^{-2} yr^{-1} for skates. During the mid-1980s, production values estimated by the inverse solution were 1.400 t km^{-2} yr^{-1} (P/B = 0.291 yr^{-1}) for small American plaice, 0.235 t km^{-2} yr^{-1} (P/B = 0.427 yr^{-1}) for large American plaice, 0.465 t km^{-2} yr^{-1} (P/B = 0.298 yr^{-1}) for flounders, and 0.017 t km^{-2} yr^{-1} (P/B = 0.219 yr^{-1}) for skates. During the mid-1990s, the modelling estimates were 1.504 t km^{-2} yr^{-1} (P/B = 0.394 yr^{-1}) for small American plaice, 0.092 t km^{-2} yr^{-1} (P/B = 0.351 yr^{-1}) for large American plaice, 0.437 t km^{-2} yr^{-1} (P/B = 0.263 yr^{-1}) for flounders, and 0.010 t km^{-2} yr^{-1} (P/B = 0.245 yr^{-1}) for skates.

Consumption

For small American plaice, a consumption estimate was obtained from a study in Passamaquoddy Bay (New Brunswick) (MacDonald and Waiwood 1987). These authors estimated a food consumption of 1.28% of body mass per day, resulting in a Q/B ratio of 4.672 yr^{-1}. When the minimum and maximum biomass values were used for each period and based on this previous Q/B ratio, this resulted in a consumption range of 17.985 to 25.299 and 15.680 to 21.035 t km^{-2} yr^{-1}, respectively, for the two periods. Based on the mean production (1.911 and 1.518 t km^{-2} yr^{-1}) for each period and the minimum and maximum GE limits (10–30%), we obtained another consumption range of 6.371 to 19.112 and 5.061 to 15.184 t km^{-2} yr^{-1} during the mid-1980s and mid-1990s, respectively. The resulting lower and upper consumption limits were thus of 6.371 to 25.299 t km^{-2} yr^{-1} and 5.061 to 21.035 t km^{-2} yr^{-1}, respectively, for the two periods. The inverse solution estimated a consumption of 8.071 t km^{-2} yr^{-1} (Q/B = 1.681 yr^{-1}) and 10.530 t km^{-2} yr^{-1} (Q/B = 2.760 yr^{-1}) for small American plaice during the mid-1980s and mid-1990s, respectively.

For large American plaice, FishBase provided an initial Q/B estimate based on fish at 2°C (Froese and Pauly 2002). The Q/B value obtained in this way was 2.0 yr^{-1}. A second estimate of consumption was derived from daily ration data using the model of Elliott and Persson (1978)

with fish from the Grand Banks of Newfoundland (Zamarro 1992). Mean daily consumptions, calculated monthly, were 0.04% to 0.64% of body mass per day, with a final mean of 0.34%. Accordingly, the mean annual Q/B ratio was 1.241 yr^{-1}. When the minimum and maximum biomass values were used for each period and based on these two previous Q/B ratios, this resulted in a consumption range of 0.542 to 1.246 and 0.286 to 0.589 t km^{-2} yr^{-1}, respectively, for the two periods. Based on the mean production (0.244 and 0.087 t km^{-2} yr^{-1}) for each period and the minimum and maximum GE limits (10–30%), we obtained another consumption range of 0.815 to 2.444 and 0.289 to 0.867 t km^{-2} yr^{-1} during the mid-1980s and mid-1990s, respectively. Assuming that this species would eat at least as much food as its biomass ($Q/B \geq 1$), the resulting lower and upper consumption limits were thus 0.549 (instead of 0.542) to 2.444 t km^{-2} yr^{-1} and 0.286 to 0.867 t km^{-2} yr^{-1}, respectively, for the two periods. The inverse solution estimated a consumption of 1.176 t km^{-2} yr^{-1} ($Q/B = 2.141$ yr^{-1}) and 0.591 t km^{-2} yr^{-1} ($Q/B = 2.262$ yr^{-1}) for large American plaice during the mid-1980s and mid-1990s, respectively.

For flounders, FishBase provided a Q/B of 2.4 yr^{-1} for winter flounder and 1.7 yr^{-1} for yellowtail flounder based on fish at 2°C (Froese and Pauly 2002). When the minimum and maximum biomass values were used for each period and based on these two previous Q/B ratios, this resulted in a consumption range of 2.078 to 4.962 and 2.281 to 5.081 t km^{-2} yr^{-1}, respectively, for the two periods. Based on the mean production (0.344 and 0.337 t km^{-2} yr^{-1}) for each period and the minimum and maximum GE limits (10–30%), we obtained another consumption range of 1.146 to 3.438 and 1.123 to 3.368 t km^{-2} yr^{-1} during the mid-1980s and mid-1990s, respectively. Assuming that these species would eat at least as much food as their biomass ($Q/B \geq 1$), the resulting lower and upper consumption limits were thus 1.561 (instead of 1.146) to 4.962 t km^{-2} yr^{-1} and 1.657 (instead of 1.123) to 5.081 t km^{-2} yr^{-1}, respectively, for the two periods. The inverse solution estimated a consumption of 2.601 t km^{-2} yr^{-1} ($Q/B = 1.666$ yr^{-1}) and 2.897 t km^{-2} yr^{-1} ($Q/B = 1.749$ yr^{-1}) for flounders during the mid-1980s and mid-1990s, respectively.

For skates, three estimates of the Q/B ratio were taken into account. The first ($Q/B = 1.2$ yr^{-1}) of these was determined from FishBase based on fish at 2°C (Froese and Pauly 2002). The second Q/B estimate was determined for thorny skates from the Barents Sea (Dolgov 1997). Estimated annual consumption from this study was divided by mean biomass, resulting in an annual Q/B ratio of 2.369 yr^{-1}. The other estimate, based on thorny skate stomachs collected in the North Sea (Vinter 1989), produced a Q/B ratio of 2.865 yr^{-1}. When the minimum and maximum biomass values were used for each period and based on the three previous Q/B ratios, this resulted in a consumption range of 0.084 to 0.270 and 0.042 to 0.132 t km^{-2} yr^{-1}, respectively, for the two periods. Based on the mean production (0.016 and 0.008 t km^{-2} yr^{-1}) for each period and the minimum and maximum GE limits (10–30%), we obtained another consumption range of 0.054 to 0.162 and 0.028 to 0.085 t km^{-2} yr^{-1} during the mid-1980s and mid-1990s, respectively. Assuming that these species would eat at least as much food as their biomass ($Q/B \geq 1$), the resulting lower and upper consumption limits were thus 0.080 (instead of 0.054) to 0.270 t km^{-2} yr^{-1} and 0.040 (instead of 0.028) to 0.132 t km^{-2} yr^{-1}, respectively, for the two periods. The inverse solution estimated a consumption of 0.095 t km^{-2} yr^{-1} ($Q/B = 1.190$ yr^{-1}) and 0.046 t km^{-2} yr^{-1} ($Q/B = 1.155$ yr^{-1}) for skates during the mid-1980s and mid-1990s, respectively.

Diet composition

Stomach content data for American plaice, flounders and skates were available from NAFO division 4T (M. Hanson, unpublished data). For American plaice, we used length-stratified samples from July to September between 1991 and 1995 (n = 946). The same diet composition was used for the two periods. Large zooplankton was the most important prey (65.2%) followed by other benthic invertebrates (15.8%) (Table 9).

For large American plaice, we used length-stratified samples from July to September between 1991 and 1995 (n = 595). These diet data were used for the two periods. The most important prey were echinoderms, large zooplankton, and polychaetes (80.9% of the diet in the mid-1990s; Table 9). However, during the mid-1980s, we also used another diet study from Langton and Bowman (1980). In that study, of 180 food-containing stomachs collected from bottom-trawl survey cruises in western Nova Scotia from 1969 to 1972, the primary prey items were echinoderms (60.4%) and large crustaceans (18.8%).

For flounders, we had summer samples from 1993 to 1997 for winter flounder (n = 963) and from 1996 to 1997 for yellowtail flounder (n = 60). These two diet compositions were weighted by the biomass of each species for each period to produce the final diet for flounders, which was used for the two periods. The most important prey were echinoderms, polychaetes, other benthic invertebrates, and molluscs (90.2% of the diet; Table 9)

The diet of the thorny skate was assumed to be representative of the entire skate group. A summer diet for thorny skate was calculated with samples from 1996 to 1998 (n = 240). These diet data were used for the two periods. The most important prey were planktivorous small pelagics and large crustaceans (76.8% of the diet; Table 9). However, during the mid-1980s, we also used another diet study from Templeman (1982). This author examined the annual diet of thorny skates from the northwest Atlantic and found that the main prey species were (by volume) small demersal feeders (25.5%), redfish (23.6%), sand lance (15.8%), large crustaceans (14.3%), and small Atlantic cod (5.7%). The resulting diet composition for skates for each period is shown in Table 9.

Table 9. Diet compositions of small and large American plaice, flounders, and skates used in modelling for each period. Est: diet estimates by the inverse model; TRN: number of trophic relations; SD: standard deviation. All values are percentages except TRN. Empty cells indicate that a prey item was never found whereas "0.0" indicates that it was found in very small amounts. Values used in data equations or as upper and lower limit constraints are indicated in boldface.

	Small American plaice					
Prey	Mean	± SD	Min	Max	Est. (mid-1980s)	Est. (mid-1990s)
Large cod						
Small cod						
Green. halibut						
Small Amer. plaice						
Large Amer. plaice						
Flounders						
Skates						
Redfish						
Large demersals						
Small demersals						
Capelin						
Large pelagics						
Pisci. small pelagics						
Plank. small pelagics						
Shrimp	3.2	9.8	**0.0**	**13.8**	0.7	5.5
Large crustacea	**0.2**	0.7	0.0	1.0	0.2	0.2
Echinoderms	**3.1**	18.0	0.0	25.5	3.1	3.1
Molluscs	**6.0**	34.5	0.0	48.7	6.0	6.0
Polychaetes	6.6	12.0	**0.0**	**16.9**	10.4	8.2
Other bent. inver.	15.8	29.1	**0.0**	**41.1**	27.5	28.3
Large zooplankton	65.2	64.3	**9.1**	**100.0**	52.0	48.6
Small zooplankton	**0.1**	0.8	0.0	1.1	0.1	0.1
Phytoplankton						
Detritus						
Total	100.0		9.1	248.2	100.0	100.0
TRN	8					

Table 9. Cont.

	Large American plaice (mid-1980s)					Large American plaice (mid-1990s)				
Prey	Mean	± SD	Min	Max	Est	Mean	± SD	Min	Max	Est
Large cod										
Small cod	**0.0**	0.1	0.0	0.1	0.0	**0.0**	0.0	0.0	0.0	0.0
Green. halibut										
Small Amer. plaice										
Large Amer. plaice										
Flounders										
Skates										
Redfish										
Large demersals										
Small demersals	**0.1**	0.2	0.0	0.3	0.1	**0.0**	0.0	0.0	0.0	0.0
Capelin	**0.0**	0.1	0.0	0.1	0.0	**0.0**	0.0	0.0	0.0	0.0
Large pelagics										
Pisci. small pelagics										
Plank. small pelagics	**0.0**	0.1	0.0	0.1	0.0	**0.0**	0.0	0.0	0.0	0.0
Shrimp	5.9	0.7	**5.5**	**6.5**	5.7	5.5	8.6	**0.0**	**12.2**	3.9
Large crustacea	7.1	12.5	**1.1**	**18.8**	1.6	1.1	3.3	**0.0**	**4.7**	0.9
Echinoderms	50.0	11.1	**44.7**	**60.4**	53.4	44.7	67.4	**0.0**	**95.2**	39.2
Molluscs	6.9	5.8	**1.4**	**9.7**	7.8	**9.7**	58.5	0.0	82.7	9.7
Polychaetes	12.7	10.8	**2.6**	**17.9**	15.3	17.9	34.4	**0.0**	**48.7**	15.7
Other bent. inver.	**2.5**	0.4	2.2	2.7	2.5	2.7	5.7	**0.0**	**8.1**	2.6
Large zooplankton	14.6	7.6	**7.5**	**18.3**	13.4	18.3	62.1	**0.0**	**87.8**	28.1
Small zooplankton	**0.0**	0.0	0.0	0.0	0.0	**0.0**	0.1	0.0	0.1	0.0
Phytoplankton										
Detritus										
Total	100.0		65.1	134.9	100.0	100.0		0.0	339.5	100.0
TRN	12					12				

Table 9. Cont.

	Flounders					
Prey	Mean	± SD	Min	Max	Est. (mid-1980s)	Est. (mid-1990s)
Large cod						
Small cod						
Green. halibut						
Small Amer. plaice						
Large Amer. plaice						
Flounders						
Skates						
Redfish						
Large demersals						
Small demersals	0.9	0.9	**0.0**	**1.3**	0.0	0.0
Capelin						
Large pelagics						
Pisci. small pelagics						
Plank. small pelagics	1.2	1.6	**0.6**	**2.9**	1.3	1.5
Shrimp	**2.4**	0.5	1.9	2.6	2.4	2.4
Large crustacea	1.6	1.6	**0.0**	**2.2**	0.0	0.4
Echinoderms	24.6	13.4	**19.5**	**38.4**	26.4	26.4
Molluscs	17.8	22.1	**9.3**	**40.6**	31.4	26.7
Polychaetes	24.5	15.7	**8.2**	**30.5**	18.8	19.2
Other bent. inver.	23.3	14.9	**7.9**	**29.0**	18.1	20.4
Large zooplankton	0.7	0.6	**0.0**	**0.9**	0.2	0.5
Small zooplankton	**0.0**	0.0	0.0	0.0	0.0	0.0
Phytoplankton						
Detritus	3.0	2.9	**0.0**	**4.1**	1.4	2.5
Total	100.0		47.5	152.5	100.0	100.0
TRN	11					

Table 9. Cont.

	Skates (mid-1980s)					Skates (mid-1990s)				
Prey	Mean	± SD	Min	Max	Est	Mean	± SD	Min	Max	Est
Large cod										
Small cod	3.3	4.0	**0.0**	**5.7**	5.5	**0.0**	0.0	0.0	0.0	0.0
Green. halibut	**0.0**	0.0	0.0	0.0	0.0	**0.0**	0.0	0.0	0.0	0.0
Small Amer. plaice	**0.1**	0.1	0.0	0.1	0.1	**0.0**	0.0	0.0	0.0	0.0
Large Amer. plaice										
Flounders	**0.5**	0.6	0.0	0.8	0.5	**0.0**	0.0	0.0	0.0	0.0
Skates										
Redfish	13.6	16.7	**0.0**	**23.6**	0.1	**0.0**	0.0	0.0	0.0	0.0
Large demersals										
Small demersals	18.6	11.4	**9.3**	**25.5**	24.1	9.3	23.3	**2.6**	**35.5**	2.6
Capelin	1.8	1.7	**0.5**	**2.8**	2.3	**0.5**	0.4	0.0	0.6	0.5
Large pelagics										
Pisci. small pelagics	2.7	3.4	**0.0**	**4.8**	4.8	**0.0**	0.0	0.0	0.0	0.0
Plank. small pelagics	**36.9**	34.3	16.2	64.8	36.9	64.8	57.6	**0.0**	**81.4**	56.0
Shrimp	3.1	3.8	**0.8**	**6.2**	5.9	6.2	2.1	**5.6**	**8.6**	7.1
Large crustacea	13.4	1.6	**12.0**	**14.3**	13.0	12.0	26.5	**4.4**	**41.9**	23.2
Echinoderms	**0.1**	0.0	0.1	0.2	0.1	**0.2**	0.1	0.0	0.2	0.2
Molluscs	**0.8**	0.1	0.7	0.9	0.8	**0.7**	0.5	0.2	0.8	0.7
Polychaetes	4.5	1.3	**3.7**	**5.6**	5.3	5.6	7.3	**3.5**	**13.8**	9.3
Other bent. inver.	**0.5**	0.3	0.3	0.7	0.5	0.7	0.61	**0.0**	**0.9**	0.5
Large zooplankton	**0.1**	0.1	0.0	0.2	0.1	**0.0**	0.0	0.0	0.0	0.0
Small zooplankton										
Phytoplankton										
Detritus										
Total	100.0		43.8	156.2	100.0	100.0		16.3	183.7	100.0
TRN	16					16				

Redfish and demersal feeders

Background

The demersal feeders represent deep-water demersal species from NAFO division 4T. Redfish was treated separately to be consistent with the northern gulf models (Morissette et al. 2003; Savenkoff et al. 2004). The remaining demersal species were divided into large and small demersal feeders.

Redfish distribution in the northwest Atlantic ranges from west Greenland in the north to the Gulf of Maine in the south (Atkinson and Melteff 1987). Two redfish species are known to be the main component of the northwest Atlantic stock: *Sebastes mentella*, which generally occupies

waters deeper than 250 m, and *Sebastes fasciatus*, usually found in shallower waters down to 300 m (Ni 1982; Rubec et al. 1991). Redfish usually inhabit waters from 100 to 700 m in depth and are ovoviviparous. Mating usually occurs in September or October, and females release live young from April to July. Redfish grow quite slowly, generally taking 8 to 10 years before being recruited to the commercial fishery at approximately 25 cm in length. This species has been commercially fished since the early 1950s, but catches have recently undergone important increases followed by dramatic declines in the early 1990s. In 4T, redfish are found almost exclusively in the deep part of the Laurentian Channel, outside of the study area.

The large demersal feeder group is mainly made up of white hake (*Urophycis tenuis*), black dogfish (*Centroscyllium fabricii*), marlin spike grenadier (*Nezumia bairdi*), Atlantic halibut (*Hippoglossus hippoglossus*), wolffish (*Anarhichas* spp.), common lumpfish (*Cyclopterus lumpus*), haddock (*Melanogrammus aeglefinus*), longfin hake (*Urophycis chesteri*), large eelpout (Zoarcidae), and monkfish (*Lophius americanus*). Information was limited for most of these species in NAFO division 4T.

The small demersal feeder group includes sculpins (Cottidae), small eelpouts (Zoarcidae), fourbeard rockling (*Enchelyopus cimbrius*), cunner (*Tautogolabrus adspersus*), gunnels (Pholidae), lumpsuckers (*Eumicrotremus* sp.), and blennies (Stichaeidae). Juvenile of large demersal feeders were also considered as small demersal feeders. Unfortunately, little is known about these species and only scant information from the study area was available.

Catch

Commercial landings of redfish in NAFO division 4T was taken from NAFO fisheries statistics (NAFO 1999). The mean annual landings in 4T were 4,505 and 1,738 t during the 1985–1987 and 1994–1996 periods, respectively. Since the study area covered only a fraction of 4T, we used the ratio of the biomass estimated in the study area (biomass in survey strata 416-438 excluding stratum 425) to the whole 4T biomass (biomass in all survey strata) for each period as a correction factor for catch. The correction factors for catch were 0.03 and 0.06, respectively, for the two periods. This resulted in mean annual catches of redfish of $2.14 \times 10^{-3} \pm 9.16 \times 10^{-4}$ and $9.78 \times 10^{-4} \pm 1.66 \times 10^{-3}$ t km^{-2} yr^{-1} in the mid-1980s and mid-1990s, respectively. The modelling catch estimate of redfish was 2.53×10^{-3} and 1.07×10^{-3} t km^{-2} yr^{-1}, respectively, for the two periods.

The landings of the large demersal feeders group were calculated by summing NAFO landing statistics for each of the species listed above (NAFO 1999). For white hake, the mean annual landings in 4T were 5,578 and 420 t during the 1985–1987 and 1994–1996 periods, respectively. The area correction factor was 0.69 and 0.60, respectively, for the two periods. For haddock, the mean annual landings in 4T were 489 and 0.3 t for the two periods and the two area correction factors were 1 and 0.60. For wolffishes, the mean annual landings in 4T were 17 and 3 t for the two periods and the two area correction factors were 0.66 and 0.77. For lumpfish, the mean annual landings in 4T were 2 and 3 t for the two periods and the two area correction factors were 0.96 and 1. Finally, for Atlantic halibut, the mean annual landings in 4T were 112 and 65 t for the two periods and the two area correction factors were 0.5 and 0.73. This resulted in a mean annual catch of large demersals of $7.03 \times 10^{-2} \pm 1.27 \times 10^{-2}$ and $5.97 \times 10^{-3} \pm 8.09 \times 10^{-3}$ t km^{-2}

yr^{-1} in the mid-1980s and mid-1990s, respectively. The modelling catch estimate of large demersals was 6.63×10^{-2} and 1.69×10^{-3} t km^{-2} yr^{-1}, respectively, for the two periods.

For the small demersal feeders, there was no fishery during the 1985–87 period and only 1 t of sculpins was landed in 1994. The catch was thus set at zero during the mid-1980s and the mean annual catch of small demersals was $5.19 \times 10^{-6} \pm 8.99 \times 10^{-6}$ t km^{-2} yr^{-1} in the mid-1990s. The modelling catch estimate of small demersals was 7.21×10^{-6} t km^{-2} yr^{-1} during the mid-1990s.

Biomass

Annual biomass estimates were obtained from the groundfish survey in the NAFO division 4T each September. The length-frequency data were corrected for catchability. Total biomass was estimated each year by multiplying the abundance estimate for each length increment by the mean weight-at-length (derived from length–weight relationships) and summing the results. During the mid-1980s, this resulted in mean biomass estimates of 1,792 t or 0.028 t km^{-2} (SD = 0.021 t km^{-2}) for redfish, 21,998 t or 0.343 t km^{-2} (SD = 0.111 t km^{-2}) for large demersals, and 5,886 t or 0.092 t km^{-2} (SD = 0.033 t km^{-2}) for small demersals. However, based on initial inverse modelling runs, the previous value for small demersals seemed to be too low to meet predator demands (see the following production section). Here we assumed that biomass was incorrect, but another possibility would be that the diet compositions of the predators (and thus the trophic relationships of the models) were incorrect. A mean biomass of 0.875 ± 1.152 t km^{-2} was used here (range: 0.061–1.690 t km^{-2}). This value was slightly lower than that used in the northern Gulf during the mid-1980s (1.343 ± 1.835 t km^{-2}; Morissette et al. 2003).

Mean biomass during the mid-1990s was estimated at 730 t or 0.011 t km^{-2} (SD = 0.004 t km^{-2}) for redfish, 5,342 t or 0.083 t km^{-2} (SD = 0.033 t km^{-2}) for large demersals, and 7,622 t or 0.119 t km^{-2} (SD = 0.006 t km^{-2}) for small demersals. However, based on initial inverse modelling runs (see the following production section), the previous values were increased for redfish (0.019 ± 0.019 t km^{-2}; range: 0.007–0.033 t km^{-2}), large demersals (0.218 ± 0.241 t km^{-2}; range: 0.056–0.397 t km^{-2}), and small demersals (0.304 ± 0.270 t km^{-2}; range: 0.114–0.495 t km^{-2}) to meet predator demands.

Production

It was assumed that for each group, production is equivalent to biomass multiplied by natural mortality (M), plus the catch (Allen 1971). Natural mortality was assumed to be 0.125 yr^{-1} for redfish, 0.130 yr^{-1} for large demersal feeders, and 0.25 yr^{-1} for small demersal feeders. The lower value for large demersal feeders was chosen because this group contains species such as black dogfish and Atlantic halibut that are slow growing, long lived, and have relatively low natural mortality rates.

During the mid-1980s, when the minimum and maximum biomass values were used for redfish, we obtained a production range of 0.002 to 0.009 t km^{-2} yr^{-1}, corresponding to a mean production value of 0.006 t km^{-2} yr^{-1} (P/B = 0.202 yr^{-1}). When the initial minimum and maximum biomass values were used during the mid-1990s, we obtained a production range of 0.001 to 0.004 t km^{-2} yr^{-1}, corresponding to a mean production value of 0.002 t km^{-2} yr^{-1} (P/B = 0.211 yr^{-1}).

However, based on initial inverse modelling runs, the previous values seemed to be too low to meet predator demands. A production of 0.007 t km^{-2} yr^{-1} was required and was thus used as the maximum production limit. This maximum production value was related to a biomass value of 0.033 t km^{-2} (see the previous biomass section). The resulting lower and upper production limits were thus 0.001 to 0.007 t km^{-2} yr^{-1} during the mid-1990s. The modelling production estimate for redfish was 0.009 and 0.007 t km^{-2} yr^{-1} during the mid-1980s and mid-1990s, respectively.

For large demersals, when the minimum and maximum biomass values were used during the mid-1980s, we obtained a production range of 0.093 to 0.135 t km^{-2} yr^{-1}, corresponding to a mean production value of 0.115 t km^{-2} yr^{-1} (P/B = 0.335 yr^{-1}). When the initial minimum and maximum biomass values were used during the mid-1990s, we obtained a production range of 0.008 to 0.031 t km^{-2} yr^{-1}, corresponding to a mean production value of 0.017 t km^{-2} yr^{-1} (P/B = 0.202 yr^{-1}). However, based on initial inverse modelling runs, the previous values seemed to be too low to meet predator demands. A production of 0.080 t km^{-2} yr^{-1} was required and was thus used as the maximum production limit. This maximum production value was related to a biomass value of 0.397 t km^{-2} (see the previous biomass section). The resulting lower and upper production limits were thus 0.008 to 0.080 t km^{-2} yr^{-1} during the mid-1990s. The modelling production estimate for large demersals was 0.122 and 0.073 t km^{-2} yr^{-1} during the mid-1980s and mid-1990s, respectively.

For small demersals, when the initial minimum and maximum biomass values were used during the mid-1980s, we obtained a production range of 0.015 to 0.032 t km^{-2} yr^{-1}, corresponding to a mean production value of 0.023 t km^{-2} yr^{-1} (P/B = 0.250 yr^{-1}). However, based on initial inverse modelling runs, the previous values seemed to be too low to meet predator demands. A production of 0.422 t km^{-2} yr^{-1} was required and was thus used as the maximum production limit. This maximum production value was related to a biomass value of 1.690 t km^{-2} (see the previous biomass section). The resulting lower and upper production limits were thus 0.015 to 0.422 t km^{-2} yr^{-1} during the mid-1980s. During the mid-1990s, when the initial minimum and maximum biomass values were used, we obtained a production range of 0.028 to 0.031 t km^{-2} yr^{-1}, corresponding to a mean production value of 0.030 t km^{-2} yr^{-1} (P/B = 0.250 yr^{-1}). However, based on initial inverse modelling runs, the previous values seemed to be too low to meet predator demands. A production of 0.124 t km^{-2} yr^{-1} was required and was thus used as the maximum production limit. This maximum production value was related to a biomass value of 0.495 t km^{-2} (see the previous biomass section). The resulting lower and upper production limits were thus 0.028 to 0.124 t km^{-2} yr^{-1} during the mid-1990s. The modelling production estimate for small demersals was 0.420 and 0.124 t km^{-2} yr^{-1} during the mid-1980s and mid-1990s, respectively.

Consumption

For redfish, FishBase was used to estimate a Q/B ratio (2.0 yr^{-1}) assuming a water temperature of 2°C (Froese and Pauly 2002). Other information on redfish consumption is available. Dolgov and Revetnyak (1990) estimated annual food consumption to biomass ratios for Barents Sea deep-water redfish (*Sebastes mentella*) that varied from a high of 6.0 yr^{-1} for fingerlings down to around 1.3 yr^{-1} for fish of 19 years of age. Since fingerlings and very young fish did not make up a significant part of the biomass, the mean Q/B of fish from 10 to 19 years

of age was computed. This produced a mean Q/B ratio of 1.49 yr^{-1}. In another study on redfish from west Greenland, it was determined that daily rations were 0.46% and 0.86% of body mass for the autumn–winter and spring–summer periods, respectively (Pedersen and Riget 1992b). These two values were averaged, which gave a mean of 0.66% body mass per day and was equivalent to a Q/B ratio of 2.409 yr^{-1}. On Georges Bank, the Q/B ratio for redfish was estimated at 7.970 yr^{-1} (Pauly 1989). When the resulting minimum and maximum biomass values were used for each period and based on these previous Q/B ratios, this resulted in a consumption range of 0.006 to 0.340 and 0.010 to 0.264 t km^{-2} yr^{-1} during the mid-1980s and mid-1990s, respectively. Based on the mean production (0.006 and 0.004 t km^{-2} yr^{-1}) for each period and the minimum and maximum GE limits (10–30%), we obtained other consumption ranges of 0.018 to 0.055 and 0.013 to 0.039 t km^{-2} yr^{-1} during the mid-1980s and mid-1990s, respectively. Assuming that this species would eat at least as much food as its biomass ($Q/B \geq 1$), the resulting lower and upper consumption limits were thus 0.028 (instead of 0.006) to 0.340 t km^{-2} yr^{-1} and 0.019 (instead of 0.010) to 0.264 t km^{-2} yr^{-1}, respectively, for the two periods. The inverse solution estimated a consumption of 0.049 t km^{-2} yr^{-1} (Q/B = 1.735 yr^{-1}) and 0.039 t km^{-2} yr^{-1} (Q/B = 2.111 yr^{-1}) for redfish during the mid-1980s and mid-1990s, respectively.

For the large demersal feeders, the only available consumption value (Q/B = 3.1 yr^{-1}) was obtained from FishBase assuming a water temperature of 2°C (Froese and Pauly 2002). When the resulting minimum and maximum biomass values were used for each period and based on this previous Q/B ratio, this resulted in consumption ranges of 0.672 to 1.321 and 0.174 to 1.230 t km^{-2} yr^{-1} during the mid-1980s and mid-1990s, respectively. Based on the mean production (0.114 and 0.044 t km^{-2} yr^{-1}) for each period and the minimum and maximum GE limits (10–30%), we obtained other consumption ranges of 0.379 to 1.136 and 0.146 to 0.439 t km^{-2} yr^{-1} during the mid-1980s and mid-1990s, respectively. Assuming that these species would eat at least as much food as their biomass ($Q/B \geq 1$), the resulting lower and upper consumption limits were thus 0.379 to 1.321 t km^{-2} yr^{-1} and 0.218 (instead of 0.146) to 1.230 t km^{-2} yr^{-1}, respectively, for the two periods. The inverse solution estimated a consumption of 0.412 t km^{-2} yr^{-1} (Q/B = 1.201 yr^{-1}) and 0.244 t km^{-2} yr^{-1} (Q/B = 1.123 yr^{-1}) for large demersals during the mid-1980s and mid-1990s, respectively.

For small demersal feeders, the only information available was obtained from FishBase assuming a water temperature of 2°C (Froese and Pauly 2002). Two Q/B ratios were estimated in this way for sea raven (1.7 yr^{-1}) and longhorn sculpin (2.0 yr^{-1}). When the resulting minimum and maximum biomass values were used for each period and based on these previous Q/B ratios, this resulted in consumption ranges of 0.104 to 3.379 and 0.193 to 1.773 t km^{-2} yr^{-1} during the mid-1980s and mid-1990s, respectively. Based on the mean production (0.219 and 0.076 t km^{-2} yr^{-1}) for each period and the minimum and maximum GE limits (10–30%), we obtained other consumption ranges of 0.729 to 2.188 and 0.254 to 0.761 t km^{-2} yr^{-1} during the mid-1980s and mid-1990s, respectively. Assuming that these species would eat at least as much food as their biomass ($Q/B \geq 1$), the resulting lower and upper consumption limits were thus 0.875 (instead of 0.104) to 3.379 t km^{-2} yr^{-1} and 0.304 (instead of 0.193) to 1.773 t km^{-2} yr^{-1}, respectively, for the two periods. The inverse solution estimated a consumption of 1.523 t km^{-2} yr^{-1} (Q/B = 1.739 yr^{-1}) and 0.415 t km^{-2} yr^{-1} (Q/B = 1.394 yr^{-1}) for small demersals during the mid-1980s and mid-1990s, respectively.

Diet composition

Stomach content data for redfish from NAFO division 4T were not available for the studied periods. Diet information for this group was taken from the northern Gulf during the mid-1990s since there was no specific diet data for the mid-1980s (Savenkoff et al. 2004). Sampling was length-stratified and covered inshore and offshore zones for all seasons from 1993 to 1999. The most important prey items of redfish were shrimp and large zooplankton (86.0% of the diet). The redfish diet from Bundy et al. (2000) in the Newfoundland–Labrador Shelf (1985–1987 period), in which the main prey items were large zooplankton (53.8%), small zooplankton (16.1%), and small planktivorous pelagics (24.5%), was also used. The final diet compositions are shown in Table 10.

For large demersal feeders, diet was assumed to be that of white hake, the key species of the group. Stomach content data for white hake was available from NAFO division 4T (M. Hanson, unpublished data). We used samples from 1996 to 2001 (n = 1,755). These diet data were used for the two periods. However, we added another source of information during the mid-1980s (Langton and Bowman 1980). The most important prey for the two periods was planktivorous small pelagic feeders (Table 10).

For small demersal feeders, we had samples for three species, longhorn sculpin (from 1994 to 1999; n = 786), shorthorn sculpin (from 1995 to 1999; n = 132), and sea raven (from 1996 to 1999; n = 67). These three diet compositions were weighted by the biomass of each species for each period to estimate the final diet composition of small demersals during each period (Table 10).

Table 10. Diet compositions of redfish, large demersal feeders, and small demersal feeders used in modelling. Est: diet estimates by the inverse model; TRN: number of trophic relations; SD: standard deviation. All values are percentages except TRN. Empty cells indicate that a prey item was never found whereas "0.0" indicates that it was found in very small amounts. Values used in data equations or as upper and lower limit constraints are indicated in boldface.

	Redfish					
Prey	Mean	± SD	Min	Max	Est. (mid-1980s)	Est. (mid-1990s)
Large cod						
Small cod	**0.3**	0.5	0.0	0.7	0.3	0.3
Green. halibut						
Small Amer. plaice						
Large Amer. plaice						
Flounders						
Skates						
Redfish	1.7	2.6	**0.0**	**3.7**	0.0	0.0
Large demersals						
Small demersals	1.6	2.5	**0.0**	**3.5**	0.3	0.0
Capelin	5.2	7.8	**0.0**	**11.1**	2.8	5.8
Large pelagics						
Pisci. small pelagics	**0.2**	0.3	0.0	0.4	0.2	0.2
Plank. small pelagics	13.9	21.1	**0.0**	**29.8**	22.3	12.4
Shrimp	37.6	52.3	**3.5**	**77.5**	28.2	40.5
Large crustacea						
Echinoderms						
Molluscs	**0.0**	0.0	0.0	0.0	0.0	0.0
Polychaetes						
Other bent. inver.	**0.0**	0.0	0.0	0.0	0.0	0.0
Large zooplankton	31.9	27.6	**14.7**	**53.8**	36.3	30.0
Small zooplankton	7.5	11.3	**0.1**	**16.1**	9.6	10.8
Phytoplankton						
Detritus						
Total	100.0		18.4	196.7	100.0	100.0
TRN	11					

Table 10. Cont.

	Large demersals (mid-1980s)					Large demersals (mid-1990s)				
Prey	Mean	± SD	Min	Max	Est	Mean	± SD	Min	Max	Est
Large cod										
Small cod	1.1	4.3	**0.5**	**6.6**	1.9	**0.5**	0.4	0.0	0.6	0.5
Green. halibut	**0.6**	0.4	0.0	0.6	0.6	**0.6**	0.5	0.0	0.7	0.6
Small Amer. plaice	**0.6**	0.4	0.0	0.6	0.6	**0.6**	0.5	0.0	0.7	0.6
Large Amer. plaice										
Flounders	**0.6**	0.4	0.0	0.6	0.6	**0.6**	0.5	0.0	0.7	0.6
Skates	**0.8**	6.7	0.0	9.4	1.0	**0.0**	0.0	0.0	0.0	0.0
Redfish	**0.4**	3.4	0.0	4.8	0.4	**0.0**	0.0	0.0	0.0	0.0
Large demersals										
Small demersals	**2.3**	10.6	1.0	16.0	2.3	**1.0**	13.7	0.1	19.5	1.0
Capelin	**0.8**	6.7	0.0	9.4	0.8	**0.0**	0.0	0.0	0.0	0.0
Large pelagics										
Pisci. small pelagics	8.9	5.7	**8.2**	**16.2**	12.8	8.2	6.3	**0.0**	**8.8**	5.0
Plank. small pelagics	75.8	38.4	**26.3**	**80.6**	71.9	80.6	61.8	**0.0**	**87.4**	83.8
Shrimp	2.5	2.7	**2.1**	**5.9**	3.1	**2.1**	20.2	0.0	28.6	2.1
Large crustacea	**0.7**	0.2	0.6	1.0	0.7	**0.6**	50.3	0.1	71.3	0.6
Echinoderms										
Molluscs										
Polychaetes	4.0	2.8	**0.3**	**4.3**	2.4	**4.3**	40.8	0.0	57.7	4.3
Other bent. inver.	**0.6**	0.1	0.5	0.6	0.6	**0.6**	5.8	0.0	8.1	0.6
Large zooplankton	**0.4**	2.2	0.1	3.3	0.4	**0.1**	1.1	0.0	1.5	0.1
Small zooplankton	**0.0**	0.2	0.0	0.2	0.0	**0.0**	0.0	0.0	0.0	0.0
Phytoplankton										
Detritus										
Total	100.0		39.7	160.3	100.0	100.0		0.2	285.6	100.0
TRN	16					16				

Table 10. Cont.

	Small demersals (mid-1980s)					Small demersals (mid-1990s)				
Prey	Mean	± SD	Min	Max	Est	Mean	± SD	Min	Max	Est
Large cod										
Small cod	6.0	10.3	**0.0**	**14.6**	7.3	**1.9**	10.3	0.0	14.6	1.9
Green. halibut										
Small Amer. plaice	11.0	20.6	**0.0**	**29.1**	29.1	2.4	20.6	**0.0**	**29.1**	25.4
Large Amer. plaice										
Flounders	8.4	14.3	**0.7**	**20.9**	11.1	2.5	14.3	**0.7**	**20.9**	14.2
Skates										
Redfish										
Large demersals										
Small demersals	17.8	15.5	**9.5**	**31.4**	9.5	11.4	15.5	**9.5**	**31.4**	9.5
Capelin	**0.3**	0.4	0.0	0.5	0.3	**0.4**	0.4	0.0	0.5	0.4
Large pelagics										
Pisci. small pelagics										
Plank. small pelagics	5.8	6.3	**0.0**	**8.9**	6.3	7.4	6.3	**0.0**	**8.9**	3.8
Shrimp	12.4	12.8	**1.7**	**19.9**	4.2	16.7	12.8	**1.7**	**19.9**	9.8
Large crustacea	15.8	57.4	**0.5**	**81.6**	2.1	25.8	57.4	**0.5**	**81.6**	15.9
Echinoderms	**0.1**	0.1	0.0	0.2	0.1	**0.2**	0.1	0.0	0.2	0.2
Molluscs	0.6	0.8	**0.0**	**1.1**	0.9	0.9	0.8	**0.0**	**1.1**	0.8
Polychaetes	11.3	13.6	**0.0**	**19.3**	16.9	15.8	13.6	**0.0**	**19.3**	7.5
Other bent. inver.	1.3	1.6	**0.0**	**2.2**	1.3	1.8	1.6	**0.0**	**2.2**	1.2
Large zooplankton	9.2	11.1	**0.0**	**15.7**	10.8	12.8	11.1	**0.0**	**15.7**	9.4
Small zooplankton										
Phytoplankton										
Detritus										
Total	100.0		12.5	245.3	100.0	100.0		12.5	245.3	100.0
TRN	13					13				

Forage fish

Background

There was very little information available on forage fish from NAFO division 4T. Capelin (*Mallotus villosus*) is a small, short-lived pelagic fish that spends most of its life offshore, moving inshore only to spawn. The species is exploited commercially in some areas and is probably the most important forage fish of the Gulf of St. Lawrence.

Arctic cod (*Boreogadus saida*) is rare in the southern Gulf. Its relative abundance in the survey increased dramatically during the cold period in the mid 1990s. However, due to its general low biomass, we included it in the capelin group, since some diet compositions of fish

predators mentioned Arctic cod as prey. Arctic cod has a circumpolar distribution and is found in the northwest Atlantic from arctic waters in the north down to the southern Gulf of St. Lawrence (Scott and Scott 1988). This species is pelagic and feeds mainly on invertebrates found in the upper part of the water column. Arctic cod is a key component of the marine food web of arctic waters (Hop et al. 1997) and an important link in the transfer of energy from zooplankton to other fish, marine mammals, and seabirds (Lilly et al. 1994).

Catch

According to NAFO fisheries statistics, mean annual landings of capelin in 4T were 185 and 127 t during the 1985–1987 and 1994–1996 periods, respectively (NAFO 1999). Since the study area covered only a fraction of 4T, we used the ratio of the biomass estimated in the study area (biomass in survey strata 416-438 excluding stratum 425) to the whole 4T biomass (biomass in all survey strata) for each period as a correction factor for catch. The correction factors for catch were 0.92 and 0.96, respectively, for the two periods. This resulted in mean annual catches of capelin of $2.89 \times 10^{-3} \pm 4.12 \times 10^{-3}$ and $1.91 \times 10^{-3} \pm 1.07 \times 10^{-3}$ t km^{-2} yr^{-1} in the mid-1980s and mid-1990s, respectively. The modelling catch estimate of capelin was 2.86×10^{-3} and 1.72×10^{-3} t km^{-2} yr^{-1}, respectively, for each of the two periods.

Biomass

Annual biomass estimates were obtained from the groundfish survey in the NAFO division 4T each September. The length-frequency data were corrected for catchability. Total biomass was estimated each year by multiplying the abundance estimate for each length increment by mean weight-at-length (derived from length–weight relationships) and summing the results. The mean biomass estimate for capelin was 8,044 t or 0.126 t km^{-2} (SD = 0.178 t km^{-2}) and 1,379,380 t or 21.528 t km^{-2} (SD = 23.787 t km^{-2}) during the mid-1980s and mid-1990s, respectively. However, during the mid-1980s, based on initial inverse modelling runs, the previous value for capelin seemed to be too low to meet predator demands (see the following production section). A mean biomass of 0.489 ± 0.690 t km^{-2} was used here (range: 0.000–0.976 t km^{-2}). The biomass estimate for the mid-1990s was a gross approximation and seemed to be too high. In fact, based on the final inverse model, the required biomass to meet predator demands was 5.596 t km^{-2} during the mid-1990s.

Production

There was no production information available in the study area. Production was assumed to be equal to biomass multiplied by natural mortality (M), plus the catch. Natural mortality was set to 0.6 yr^{-1} to better reflect the biology of this short-lived species (F. Grégoire, DFO, Institut Maurice-Lamontagne, Mont-Joli, Québec, personal communication). When the minimum and maximum biomass values were used during the mid-1980s, we obtained a production range of 0.001 to 0.205 t km^{-2} yr^{-1}, corresponding to a mean production value of 0.078 t km^{-2} yr^{-1} (P/B =

0.623 yr^{-1}). However, based on initial inverse modelling runs, the previous values seemed to be too low to meet predator demands. A production of 0.608 t km^{-2} yr^{-1} was required and was thus used as the maximum production limit. This maximum production value was related to a biomass value of 0.976 t km^{-2} (see previous biomass section). The resulting lower and upper production limits were thus 0.001 to 0.608 t km^{-2} yr^{-1} during the mid-1980s.

When the initial minimum and maximum biomass values were used for the mid-1990s, we obtained a production range of 2.305 to 29.287 t km^{-2} yr^{-1}, corresponding to a mean production value of 11.317 t km^{-2} yr^{-1} (P/B = 0.526 yr^{-1}).

The modelling production estimate for capelin was 0.549 and 2.942 t km^{-2} yr^{-1} during the mid-1980s and mid-1990s, respectively. Thus, based on the initial P/B ratio of 0.526 yr^{-1}, the required biomass to meet predator demands was 5.596 t km^{-2} during the mid-1990s (see previous biomass section).

Consumption

Consumption rate for capelin was taken from various sources. A Q/B ratio (3.8 yr^{-1}) was determined using FishBase for a water temperature of 1°C, considering that this species is generally found near the cold intermediate layer in the Gulf of St. Lawrence (Froese and Pauly 2002). We used a second estimate based on the feeding ecology of capelin in the estuary and western Gulf of St. Lawrence (Vesin et al. 1981). The daily ration was estimated at 5.00% body mass in summer and 2.50% body mass in winter, giving a mean of 3.75% of body mass per day. From these values, the mean annual Q/B ratio was estimated to be 13.688 yr^{-1}. A third Q/B estimate was determined from a summer study on Barents Sea capelin (Ajiad and Pushaeva 1991). Daily ration was estimated to be between 1.47% and 2.00% of the body mass, resulting in an average Q/B ratio of 6.333 yr^{-1}. Finally, Panasenko (1981) estimated a Q/B ratio of 27.558 yr^{-1} in another study in the Barents Sea.

When the resulting minimum and maximum biomass values were used for the mid-1980s and based on these previous Q/B ratios, this resulted in a consumption range of 0.000 to 26.882 t km^{-2} yr^{-1}. During the mid-1990s, when the initial minimum and maximum biomass values were used, we obtained a consumption range of 19.411 to 1,344.989 t km^{-2} yr^{-1}. Based on the mean production (0.304 and 11.317 t km^{-2} yr^{-1}) for each period and the minimum and maximum GE limits (10–30%), we obtained other consumption ranges of 1.015 to 3.044 and 37.722 to 113.167 t km^{-2} yr^{-1} during the mid-1980s and mid-1990s, respectively. Assuming that this species would eat at least as much food as its biomass (Q/B $\geq$ 1), the resulting lower and upper consumption limits were thus 0.489 (instead of 0.000) to 26.882 t km^{-2} yr^{-1} and 21.528 (instead of 19.411) to 1,344.989 t km^{-2} yr^{-1}, respectively, for the two periods. The inverse solution estimated a consumption of 2.674 t km^{-2} yr^{-1} (Q/B = 5.474 yr^{-1}) and 22.617 t km^{-2} yr^{-1} (Q/B = 1.051 yr^{-1} or 4.041 if we used the estimated biomass of 5.596 t km^{-2}) for capelin during the mid-1980s and mid-1990s, respectively.

Diet composition

For capelin, we used the diet composition estimated by Vésin et al. (1981) in the Estuary and western Gulf of St. Lawrence from 1974 to 1975. In that study, euphausiids and copepods were the main prey (6.3 and 93.7%, respectively) (Table 11).

Table 11. Diet composition of capelin in modelling for each period. Est: diet estimates by the inverse model; TRN: number of trophic relations; SD: standard deviation. All values are percentages except TRN. Groups with indicated CV (available only as point estimates): Min = mean – (mean x 50%), Max = mean + (mean x 50%). Empty cells indicate that a prey item was never found whereas "0.0" indicates that it was found in very small amounts. Values used in data equations or as upper and lower limit constraints are indicated in boldface.

	Capelin (CV= 50%)					
Prey	Mean	± SD	Min	Max	Est. (mid-1980s)	Est. (mid-1990s)
Large cod						
Small cod						
Green. halibut						
Small Amer. plaice						
Large Amer. plaice						
Flounders						
Skates						
Redfish						
Large demersals						
Small demersals						
Capelin	**0.0**		0.0	0.0	0.0	0.0
Large pelagics						
Pisci. small pelagics						
Plank. small pelagics						
Shrimp						
Large crustacea						
Echinoderms						
Molluscs						
Polychaetes						
Other bent. inver.	**0.0**		0.0	0.0	0.0	0.0
Large zooplankton	6.3		**3.1**	**9.4**	6.7	6.0
Small zooplankton	93.7		**46.9**	**100.0**	93.3	94.0
Phytoplankton						
Detritus						
Total	100.0		50.0	109.4	100.0	100.0
TRN	4					

Pelagic feeders

Background

The pelagic feeders are also an important part of the ecosystem, and some species are commercially fished. Three boxes are designed to represent these species: large pelagic feeders, piscivorous small pelagic feeders, and planktivorous small pelagic feeders.

The large pelagic feeders group includes spiny dogfish (*Squalus acanthias*), pollock (*Pollachius virens*), and silver hake (*Merluccius bilinearis*). The most abundant large pelagic feeder in NAFO division 4T was spiny dogfish (especially in 1994–96 period, where it made up 98% of the biomass).

The piscivorous small pelagic feeders group includes Atlantic mackerel (*Scomber scombrus*), short-finned squid (*Illex illecebrosus*), and juvenile large pelagics. Atlantic mackerel is the most important in terms of biomass (at least 92% of the biomass) and was therefore considered the key species for the group. Mackerel populations in the northwest Atlantic form a complex stock that overwinters off the New England coast and then migrates northwards in May and June after spawning in the New Jersey Bight area and the southern Gulf of St. Lawrence (Moores et al. 1975). After spawning near the Îles-de-la-Madeleine, they disperse throughout the Gulf for the rest of the summer.

The planktivorous small pelagic feeders group includes Atlantic herring (*Clupea harengus*), Atlantic argentine (*Argentina silus*), planktivorous myctophids, sand lance (northern sand lance *Ammodytes dubius* and American sand lance *Ammodytes americanus*), and other mesopelagics (rainbow smelt, alewife, etc.). Atlantic herring is the most important in terms of biomass (at least 70% of the biomass) and was therefore considered the key species for the group.

Catch

The landings of the large pelagic feeders were calculated by summing NAFO landing statistics for each of the species listed above (NAFO 1999). For silver hake, there were no landings in 4T during the 1985–1987 period, while the mean annual landings were 0.3 t during the 1994–1996 period. Since the study area covered only a fraction of 4T, we used the ratio of the biomass estimated in the study area (biomass in survey strata 416-438 excluding stratum 425) to the whole 4T biomass (biomass in all survey strata) as a correction factor for catch for this period. The correction factor for catch was 0.42 for the mid-1990s. For pollock, the mean annual landings in 4T were 479 and 11 t, respectively, for each of the two periods, and the two area correction factors were 0.44 and 0.68. Finally, for spiny dogfish, the mean annual landings in 4T were 7 and 633 t, respectively, for each of the two periods, and the two area correction factors were 0.85 and at 0.98. This resulted in mean annual catches of large pelagics of $2.45 \times 10^{-3} \pm 2.47 \times 10^{-3}$ and $9.76 \times 10^{-3} \pm 4.85 \times 10^{-3}$ t km^{-2} yr^{-1} in the mid-1980s and mid-1990s, respectively. The modelling catch estimate of large pelagics was 2.42×10^{-3} and 1.04×10^{-2} t km^{-2} yr^{-1}, respectively, for each of the two periods.

The landings of the piscivorous small pelagic feeders were also calculated by summing NAFO landing statistics for each of the species listed above (NAFO 1999). For Atlantic mackerel, the mean annual landings in 4T were 9,896 and 9,971 t during the 1985–1987 and

1994–1996 periods, respectively, and the area correction factor was 1.00 for the two periods. For short-finned squid, there were no landings in 4T during the 1985–1987 period while the mean annual landings were 28 t during the 1994–1996 period. The area correction factor was 0.63 during the mid-1990s. This resulted in mean annual catches of piscivorous small pelagics of 1.42 x 10^{-1} ± 3.86 x 10^{-2} and 1.44 x 10^{-1} ± 2.34 x 10^{-2} t km^{-2} yr^{-1} in the mid-1980s and mid-1990s, respectively. The modelling catch estimate of piscivorous small pelagics was 1.29 x 10^{-1} and 1.46 x 10^{-1} t km^{-2} yr^{-1}, respectively, for each of the two periods.

Finally, for the planktivorous small pelagic feeders group, the landings were also calculated by summing NAFO landing statistics for each of the species listed above (NAFO 1999). For Atlantic herring, the mean annual landings in 4T were 58,361 and 82,990 t during the 1985–1987 and 1994–1996 periods, respectively, and the area correction factor was 1.00 for the two periods. For rainbow smelt, the mean annual landings in 4T were 1,609 and 1,106 t during the 1985–1987 and 1994–1996 periods, respectively, and the area correction factor was 1.00 for the two periods. For alewife, the mean annual landings in 4T were 5,233 and 3,266 t during the 1985–1987 and 1994–1996 periods, respectively, and the area correction factor was 1.00 for the two periods. This resulted in mean annual catches of planktivorous small pelagics of 1.02 ± 3.18 x 10^{-1} and 1.36 ± 1.22 x 10^{-1} t km^{-2} yr^{-1} in the mid-1980s and mid-1990s, respectively. The modelling catch estimate of planktivorous small pelagics was 9.57 x 10^{-1} and 1.36 t km^{-2} yr^{-1}, respectively, for each of the two periods.

Biomass

For the large pelagic feeders group, biomass was calculated from the groundfish survey conducted in the division 4T each September. The length-frequency data were corrected for catchability. Total biomass was estimated each year by multiplying the abundance estimate for each length increment by the mean weight-at-length (derived from length–weight relationships) and summing the results. This resulted in mean biomass estimates of 1,774 t or 0.028 t km^{-2} (SD = 0.010 t km^{-2}) and 8,976 t or 0.140 t km^{-2} (SD = 0.088 t km^{-2}) during the mid-1980s and mid-1990s, respectively.

Biomass estimates for Atlantic mackerel were derived from an egg production index calculated for 1983 to 2000 for the southern Gulf of St. Lawrence (DFO 2002c). These estimates are for the spawning stock only (ages 1–2 yr; L_{50} mean = 282 mm for the 1975-2002 data) and will be under-estimates if some mackerel spawn prior to entering the Gulf (DFO 2002c). No estimates of the biomass of juvenile mackerel were available. We did not apply a residence time factor to reduce biomass by two (6 months outside the Gulf) because these fish feed mainly during the summer period when they are in the Gulf. After spawning near the Îles-de-la-Madeleine, mackerel in the Gulf disperse throughout the entire area (NAFO divisions 4RS and 4T). There is little information about the proportion of mackerel that moves into the northern (4RS) versus southern (4T) Gulf. We assumed that one third of the biomass moved into 4RS while the other two thirds was distributed in 4T. Biomass for other species was estimated from the scientific research survey and corrected for catchability. The mean biomass estimates for piscivorous small pelagics were 316,089 t or 4.933 t km^{-2} (SD = 1.700 t km^{-2}) and 74,125 t or 1.157 t km^{-2} (SD = 0.895 t km^{-2}) during the mid-1980s and mid-1990s, respectively.

For the planktivorous small pelagic feeders group, the average biomass of herring (the key species for the group) was taken from the sequential population analysis (SPA) (Leblanc et al. 2001). The spring and autumn spawner biomasses were used in the estimate (ages 2 to 11 years and older). Biomass for other species was estimated from the research survey and corrected for catchability. The mean biomass estimates for planktivorous small pelagics were 625,027 t or 9.755 t km^{-2} (SD = 1.816 t km^{-2}) and 475,513 t or 7.421 t km^{-2} (SD = 0.152 t km^{-2}) during the mid-1980s and mid-1990s, respectively.

Production

Since there was no specific information on P/B ratios for these species in the study area, it was assumed that production was equal to biomass multiplied by natural mortality (M), plus the catch. For the large pelagic feeders, natural mortality was assumed to be 0.15 yr^{-1} because one of the principal species, spiny dogfish, is a large, long-living fish with a relatively low natural mortality (Scott and Scott 1988). When the minimum and maximum biomass values were used for each period, we obtained a production range of 0.003 to 0.011 and 0.015 to 0.044 t km^{-2} yr^{-1}, respectively, for each of the two periods. The modelling estimates were 0.009 t km^{-2} yr^{-1} (P/B = 0.322 yr^{-1}) and 0.036 t km^{-2} yr^{-1} (P/B = 0.258 yr^{-1}) during the mid-1980s and mid-1990s, respectively.

For the piscivorous small pelagic feeders, in the absence of better information, a value of 0.2 yr^{-1} was used for natural mortality (F. Grégoire, DFO, Institut Maurice-Lamontagne, Mont-Joli, Québec, personal communication). For squid, a value of 1.0 yr^{-1} was used for natural mortality. When the minimum and maximum biomass values were used for each period, we obtained a production range of 0.749 to 1.537 and 0.275 to 0.533 t km^{-2} yr^{-1}, respectively, for each period. The modelling estimates were 1.247 t km^{-2} yr^{-1} (P/B = 0.253 yr^{-1}) and 0.428 t km^{-2} yr^{-1} (P/B = 0.370 yr^{-1}) during the mid-1980s and mid-1990s, respectively.

For the planktivorous small pelagic feeders, natural mortality was assumed to be 0.20 yr^{-1} for herring (Leblanc et al. 2001) and 0.44 yr^{-1} for rainbow smelt and alewife. When the minimum and maximum biomass values were used for each period, we obtained a production range of 2.710 to 3.922 and 2.789 to 3.121 t km^{-2} yr^{-1}, respectively, for each of the two periods. The modelling estimates were 3.433 t km^{-2} yr^{-1} (P/B = 0.352 yr^{-1}) and 3.036 t km^{-2} yr^{-1} (P/B = 0.409 yr^{-1}) during the mid-1980s and mid-1990s, respectively.

Consumption

For large pelagic feeders, FishBase made available one Q/B estimate (4.760 yr^{-1}) for pollock from Canadian waters and one Q/B estimate (4.770 yr^{-1}) for spiny dogfish also from Canadian waters (Froese and Pauly 2002). In another study, Cohen and Grosselin (1981) examined food consumption of fish from Georges Bank and estimated a Q/B ratio of 9.516 yr^{-1} for pollock. When the minimum and maximum biomass values during the mid-1980s and these previous Q/B ratios were used, a consumption range of 0.085 to 0.354 t km^{-2} $yr^{-1}$was obtained. During the mid-1990s, when the initial minimum and maximum biomass values and the previous Q/B ratios were used, we obtained a consumption range of 0.311 to 2.254 t km^{-2} yr^{-1}. Based on

the mean production (0.006 and 0.030 t km^{-2} yr^{-1}) for each period and the minimum and maximum GE limits (10–30%), we calculated other consumption ranges of 0.022 to 0.065 and 0.100 to 0.300 t km^{-2} yr^{-1} during the mid-1980s and mid-1990s, respectively. Assuming that these species would eat at least as much food as their biomass ($Q/B \geq 1$), the resulting lower and upper consumption limits were thus 0.028 (instead of 0.022) to 0.354 t km^{-2} yr^{-1} and 0.140 (instead of 0.100) to 2.254 t km^{-2} yr^{-1}, respectively, for the two periods. The inverse solution estimated a consumption of 0.044 t km^{-2} yr^{-1} (Q/B = 1.606 yr^{-1}) and 0.148 t km^{-2} yr^{-1} (Q/B = 1.058 yr^{-1}) for large pelagic feeders during the mid-1980s and mid-1990s, respectively.

For piscivorous small pelagic feeders, information was gathered from two sources. Mehl and Westgard (1983) estimated mackerel consumption in the North Sea to be 6% of body mass per day (N = 3,674). A Q/B ratio of 2.190 yr^{-1} was thus estimated from this information. Also, a Q/B value of 4.400 yr^{-1} for Atlantic mackerel was taken from Pauly (1989). When the minimum and maximum biomass values during the mid-1980s and these previous Q/B ratios were used, a consumption range of 7.366 to 29.647 t km^{-2} yr^{-1} was obtained. During the mid-1990s, when the initial minimum and maximum biomass values and the previous Q/B ratios were used, a consumption range of 1.147 to 7.876 t km^{-2} yr^{-1} was obtained. Based on the mean production (1.093 and 0.399 t km^{-2} yr^{-1}) for each period and the minimum and maximum GE limits (10–30%), we obtained other consumption ranges of 3.643 to 10.930 and 1.329 to 3.986 t km^{-2} yr^{-1} during the mid-1980s and mid-1990s, respectively. Assuming that these species would eat at least as much food as their biomass ($Q/B \geq 1$), the resulting lower and upper consumption limits were 4.933 (instead of 3.643) to 29.647 t km^{-2} yr^{-1} and 1.157 (instead of 1.147) to 7.876 t km^{-2} yr^{-1}, respectively, for the two periods. The inverse solution estimated a consumption of 6.750 t km^{-2} yr^{-1} (Q/B = 1.368 yr^{-1}) and 2.637 t km^{-2} yr^{-1} (Q/B = 2.279 yr^{-1}) for piscivorous small pelagic feeders during the mid-1980s and mid-1990s, respectively.

For planktivorous small pelagics, Q/B estimates were derived from Pauly (1989), Rudstam et al. (1992), and Fetter and Davidjuka (1996). During summer, specific consumption rates of herring in the Baltic Sea were estimated to be from 10 to 20% of the body mass per day for young-of-the-year fish larger than 5 cm, 7 to 13% for 1+ fish, and 4 to 5% for older age groups (Rudstam et al. 1992). During autumn, these consumption rates declined to 2 to 4% for all age classes. This resulted in an estimated annual Q/B of 13.688 yr^{-1}. Values taken from Pauly (1989) were 4.590 yr^{-1} for fish from Georges Bank and 10.100 yr^{-1} for fish from the North Sea. Finally, Fetter and Davidjuka (1996) estimated daily food consumption for different periods of the year. Mean values fluctuated widely between 0.2 and 1.3% of body mass per day, corresponding to an annual Q/B of 2.798 yr^{-1}. When the minimum and maximum biomass values during the mid-1980s and the previous Q/B ratios were used, a consumption range of 24.020 to 162.151 t km^{-2} yr^{-1} was obtained. During the mid-1990s, when the initial minimum and maximum biomass values and the previous Q/B ratios were used, a consumption range of 20.393 to 103.839 t km^{-2} yr^{-1} was obtained. Based on the mean production (3.215 and 2.946 t km^{-2} yr^{-1}) for each period and the minimum and maximum GE limits (10–30%), we obtained other consumption ranges of 10.716 to 32.149 and 9.819 to 29.457 t km^{-2} yr^{-1} during the mid-1980s and mid-1990s, respectively. The resulting lower and upper consumption limits were thus 10.716 to 162.151 t km^{-2} yr^{-1} and 9.819 to 103.839 t km^{-2} yr^{-1}, respectively, for the two periods. The inverse solution estimated a consumption of 19.858 t km^{-2} yr^{-1} (Q/B = 2.036 yr^{-1}) and 19.667 t km^{-2} yr^{-1} (Q/B = 2.650 yr^{-1}) for planktivorous small pelagic feeders during the mid-1980s and mid-1990s, respectively.

Diet composition

The diet of the large pelagic feeders was assumed to be that of spiny dogfish and pollock. For spiny dogfish, stomach content data were available from NAFO division 4T from 1996 to 1997 (n = 48) (M. Hanson, unpublished data). For pollock, we used the diet composition estimated from Langton and Bowman (1980) on the Scotian Shelf. These two diet compositions were weighted by the biomass of each species for each period to obtain the final diet composition for large pelagic feeders (Table 12).

Diet composition for the piscivorous small pelagic feeders were derived from two sources of information on Atlantic mackerel, the key species for this group. Stomach content data for mackerel were available from NAFO division 4T from June to September 1999 (n = 515) (M. Hanson, unpublished data). We used these diet data for the two periods. However, for the mid-1980s, we also used the diet composition estimated for the Gulf of St. Lawrence and the Scotian Shelf (n = 359) from Grégoire and Castonguay (1989). The resulting diet composition for the piscivorous small pelagic feeders is shown in Table 12.

For the diet of the planktivorous small pelagics, we used the diet composition from two sources of information on herring, the key species for this group. Stomach content data for herring were available from NAFO division 4T from April to September 1999 (n = 718) (M. Hanson, unpublished data). We used these diet data for the two periods. However, for the mid-1980s, we also used the diet composition estimated for the Newfoundland–Labrador Shelf (Bundy et al. 2000). The resulting diet composition for the planktivorous small pelagics is shown in Table 12.

Table 12. Diet compositions of large pelagic feeders, piscivorous small pelagic feeders, and planktivorous small pelagic feeders used in modelling. Est: diet estimates by the inverse model; TRN: number of trophic relations; SD: standard deviation. All values are percentages except TRN. Empty cells indicate that a prey item was never found whereas "0.0" indicates that it was found in very small amounts. Values used in data equations or as upper and lower limit constraints are indicated in boldface.

	Large pelagic feeders (mid-1980s)					Large pelagic feeders (mid-1990s)				
Prey	Mean	± SD	Min	Max	Est	Mean	± SD	Min	Max	Est
Large cod										
Small cod	**0.2**	0.2	0.0	0.3	0.2	**0.0**	0.2	0.0	0.3	0.0
Green. halibut										
Small Amer. plaice										
Large Amer. plaice										
Flounders	3.1	5.1	**0.0**	**7.2**	4.8	7.0	5.1	**0.0**	**7.2**	6.9
Skates	2.9	3.7	**0.0**	**5.2**	2.7	**0.1**	3.7	0.0	5.2	0.1
Redfish	0.7	0.9	**0.0**	**1.3**	0.0	**0.0**	0.9	0.0	1.3	0.0
Large demersals										
Small demersals	4.0	2.4	**2.0**	**5.5**	2.8	2.1	2.4	**2.0**	**5.5**	2.0
Capelin	3.1	3.9	**0.0**	**5.5**	2.6	**0.1**	3.9	0.0	5.5	0.1
Large pelagics										
Pisci. small pelagics	3.1	3.9	**0.0**	**5.5**	4.3	**0.1**	3.9	0.0	5.5	0.1
Plank. small pelagics	45.8	50.9	**14.4**	**86.3**	47.3	84.5	50.9	**14.4**	**86.3**	85.2
Shrimp	3.0	3.7	**0.0**	**5.3**	1.4	**0.1**	3.7	0.0	5.3	0.1
Large crustacea	1.2	1.5	**0.0**	**2.1**	0.5	**0.1**	1.5	0.0	2.1	0.1
Echinoderms										
Molluscs										
Polychaetes	2.0	3.1	**0.1**	**4.5**	3.1	4.3	3.1	**0.1**	**4.5**	3.9
Other bent. inver.	**0.0**	0.0	0.0	0.1	0.0	**0.0**	0.0	0.0	0.1	0.0
Large zooplankton	30.7	38.6	**0.0**	**54.6**	30.2	**1.3**	38.6	0.0	54.6	1.3
Small zooplankton	**0.0**	0.0	0.0	0.1	0.0	**0.0**	0.0	0.0	0.1	0.0
Phytoplankton										
Detritus										
Total	100.0		16.6	183.4	100.0	100.0		16.6	183.4	100.0
TRN	14					14				

Table 12. Cont.

Prey	Pisci. small pelagic (mid-1980s)					Pisci. small pelagic (mid-1990s)				
	Mean	± SD	Min	Max	Est	Mean	± SD	Min	Max	Est
Large cod										
Small cod										
Green. halibut										
Small Amer. plaice										
Large Amer. plaice										
Flounders										
Skates										
Redfish										
Large demersals										
Small demersals										
Capelin	6.7	8.0	**0.0**	**11.4**	0.0	11.4	16.0	**0.0**	**22.7**	18.8
Large pelagics										
Pisci. small pelagics	**0.0**	0.0	0.0	0.0	0.0	**0.0**	0.0	0.0	0.0	0.0
Plank. small pelagics	5.3	6.3	**0.0**	**8.9**	5.4	8.9	32.1	**0.0**	**45.4**	5.0
Shrimp	5.1	6.1	**0.0**	**8.6**	0.0	**8.6**	57.0	0.0	80.6	8.6
Large crustacea										
Echinoderms										
Molluscs										
Polychaetes										
Other bent. inver.	**0.4**	0.4	0.0	0.6	0.4	**0.6**	6.8	0.0	9.7	0.6
Large zooplankton	24.2	17.0	**14.3**	**38.4**	34.1	14.3	52.8	**0.0**	**74.6**	19.7
Small zooplankton	58.4	3.8	**56.2**	**61.6**	60.0	56.2	68.3	**3.4**	**100.0**	47.3
Phytoplankton										
Detritus										
Total	100.0		70.5	129.5	100.0	100.0		3.4	333.0	100.0
TRN	7					7				

Table 12. Cont.

	Plank. small pelagic (mid-1980s)					Plank. small pelagic (mid-1990s)				
Prey	Mean	± SD	Min	Max	Est	Mean	± SD	Min	Max	Est
Large cod										
Small cod										
Green. halibut										
Small Amer. plaice										
Large Amer. plaice										
Flounders										
Skates										
Redfish										
Large demersals										
Small demersals										
Capelin										
Large pelagics										
Pisci. small pelagics										
Plank. small pelagics										
Shrimp	**0.3**	0.5	0.0	0.7	0.3	**0.7**	9.7	0.0	13.7	0.7
Large crustacea										
Echinoderms										
Molluscs										
Polychaetes										
Other bent. inver.	6.1	7.1	**0.0**	**10.0**	5.3	**0.0**	2.0	0.0	2.8	0.0
Large zooplankton	41.6	17.5	**26.5**	**51.3**	36.2	26.5	66.2	**0.0**	**93.7**	40.8
Small zooplankton	52.0	24.1	**38.7**	**72.8**	58.3	72.8	70.7	**0.0**	**100.0**	58.5
Phytoplankton										
Detritus										
Total	100.0		65.3	134.7	100.0	100.0		0.0	210.2	100.0
TRN	4					4				

Crustaceans

Background

American lobster (*Homarus americanus*) were not included in the model because they are found mainly in the infra-littoral zone (Hanson and Lanteigne 2000). This zone was excluded from the model because exchanges between infra-littoral and pelagic zones are still poorly understood. The main crustaceans of the southern Gulf of St. Lawrence ecosystem are shrimp and snow crab. Both are exploited commercially.

The shrimp group consisted almost entirely of species of caridean shrimp. The northern shrimp, *Pandalus borealis*, which is fished commercially, *Pasiphaea multidentata*, and *P. tarda*

are found in the deep waters of the Laurentian Channel. The dominant shrimp species in shallower areas are the striped shrimp, *Pandalus montagui*, *Argis dentata*, *Eualus macilentus*, and *Sabinea septemcarinata* (Squires 1990; Hanson and Lanteigne 1999).

The snow crab (*Chionoecetes opilio*) represented the key species of the large crustacean group, which also included other species such as toad crabs (*Hyas coarctatus* and *H. araneus*). The snow crab fishery in the southern Gulf of St. Lawrence is one of the most valuable fisheries in Atlantic Canada (Hébert et al. 2002), after lobster.

Catch

Information on average commercial landings for shrimp in the NAFO statistics were 149 and 422 t during the mid-1980s and mid-1990s, respectively, corresponding to mean landings of $2.33 \times 10^{-3} \pm 1.49 \times 10^{-3}$ and $6.58 \times 10^{-3} \pm 6.09 \times 10^{-3}$ t km^{-2} yr^{-1} (NAFO 1999). The modelling catch estimate of shrimp was 2.11×10^{-3} and 6.62×10^{-3} t km^{-2} yr^{-1}, respectively, for each of the two periods.

For snow crab, average commercial landings in the NAFO statistics were 24,877 and 23,762 t during the mid-1980s and mid-1990s, respectively, corresponding to mean landings of $3.88 \times 10^{-1} \pm 1.24 \times 10^{-1}$ and $3.71 \times 10^{-1} \pm 4.68 \times 10^{-2}$ t km^{-2} yr^{-1} (NAFO 1999). The modelling catch estimate of large crustacea was 3.48×10^{-1} and 3.67×10^{-1} t km^{-2} yr^{-1}, respectively, for each of the two periods.

Biomass

Shrimp biomass for the southern Gulf was estimated by the groundfish survey each September. The biomass was not corrected for catchability. Mean biomass was 55 t or 0.001 t km^{-2} (SD = 0.001 t km^{-2}, range: 0.000–0.001 t km^{-2}) and 2,766 t or 0.043 t km^{-2} (SD = 0.017 t km^{-2}, range: 0.026–0.059 t km^{-2}) during the mid-1980s and mid-1990s, respectively. However, based on initial inverse modelling runs (see the following production section), the previous values were increased during the mid-1980s (0.355 ± 0.501 t km^{-2}; range: 0.000–0.709 t km^{-2}) and the mid-1990s (0.744 ± 1.028 t km^{-2}; range: 0.026–1.479 t km^{-2}) to meet predator demands.

A post-fishing season trawl survey for snow crab is conducted in snow crab fishing areas 12, E, and F (Hébert et al. 2002). In Area 12, the survey has been conducted every year since 1988 except in 1996. The abundance at length (E. Wade, DFO, Moncton, pers. comm.) for female and male snow crab was converted to biomass using a weight–length relation (B. Sainte-Marie, DFO, Mont-Joli, pers. comm.). The total biomasses for females and males are 169,975 t, 178,524 t, 217,717 t, and 149,254 t for 1988, 1989, 1994, and 1995, respectively. The surveys in 1988 and 1989 were used to estimate biomass during the mid-1980s. This resulted in a mean biomass of 174,250 t or 2.719 t km^{-2} (SD = 0.094 t km^{-2}) and 183,485 t or 2.864 t km^{-2} (SD = 0.756 t km^{-2}) during the mid-1980s and mid-1990s, respectively. However, based on initial inverse modelling runs (see the following production section), the previous values were slightly increased during the mid-1980s (2.993 ± 0.498 t km^{-2}; range: 2.653–3.357 t km^{-2}) to meet predator demands. We assumed that this range should account for the biomass of other crab species.

Production

Due to the lack of information, it was assumed that production was equal to biomass multiplied by natural mortality (M), plus the catch. For shrimp, natural mortality was assumed to be 0.64 yr^{-1} to take into account the high natural mortality of juveniles as well as the lower natural mortality of adults (Fréchette and Labonté 1981). When the initial minimum and maximum biomass values were used during the mid-1980s, we obtained a production range of 0.001 to 0.005 t km^{-2} yr^{-1}, corresponding to a mean production value of 0.003 t km^{-2} yr^{-1} (P/B = 3.272 yr^{-1}). However, catchability of shrimp in the groundfish survey trawl is expected to be very low, so these will be underestimates. Initial inverse modelling runs confirmed that these values were too low to meet predator demands. A production of 2.320 t km^{-2} yr^{-1} was required and was thus used as the maximum production limit. This maximum production value was related to a biomass value of 0.709 t km^{-2} (see previous biomass section). The resulting lower and upper production limits were 0.001 to 2.320 t km^{-2} yr^{-1} during the mid-1980s. During the mid-1990s, when the initial minimum and maximum biomass values were used, we obtained a production range of 0.030 to 0.039 t km^{-2} yr^{-1}, corresponding to a mean production value of 0.034 t km^{-2} yr^{-1}. Again, these are expected to be underestimates, and initial inverse modelling runs confirmed that these values were too low to meet predator demands. A production of 4.838 t km^{-2} yr^{-1} was required and was used as the maximum production limit. This maximum production value was related to a biomass value of 1.479 t km^{-2} based on a P/B of 3.272 yr^{-1} (see the previous biomass section). The resulting lower and upper production limits were 0.030 to 4.838 t km^{-2} yr^{-1} during the mid-1990s. The modelling production estimate for shrimp was 1.614 and 2.414 t km^{-2} yr^{-1} during the mid-1980s and mid-1990s, respectively.

For snow crab, an assumed natural mortality of 0.2 yr^{-1} was used to take into account the high natural mortality of juveniles as well as the lower natural mortality of adults (B. Sainte-Marie, DFO, Mont-Joli, personal communication). When the initial minimum and maximum biomass values were used during the mid-1980s, we obtained a production range of 0.739 to 0.790 t km^{-2} yr^{-1}, corresponding to a mean production value of 0.764 t km^{-2} yr^{-1} (P/B = 0.281 yr^{-1}). However, based on initial inverse modelling runs, the previous values seemed to be too low to meet predator demands. A production of 0.944 t km^{-2} yr^{-1} was required and was used as the maximum production limit. This maximum production value was related to a biomass value of 3.357 t km^{-2} (see the previous biomass section). The resulting lower and upper production limits were 0.739 to 0.944 t km^{-2} yr^{-1} during the mid-1980s. During the mid-1990s, when the minimum and maximum biomass values were used, we obtained a production range of 0.823 to 1.074 t km^{-2} yr^{-1}. The modelling estimates were 0.921 t km^{-2} yr^{-1} (P/B = 0.308 yr^{-1}) and 0.972 t km^{-2} yr^{-1} (P/B = 0.339 yr^{-1}) during the mid-1980s and mid-1990s, respectively.

Consumption

In the absence of information on food consumption by shrimp, consumption was only estimated by using the gross growth efficiency (GE, the ratio of production to consumption). Based on the mean production (1.161 and 2.434 t km^{-2} yr^{-1}) for each period and the minimum and maximum GE limits (10–30%), we obtained a consumption range of 3.869 and 11.607 t km^{-2} yr^{-1}

and 8.113 to 24.340 t km^{-2} yr^{-1} during the mid-1980s and mid-1990s, respectively. The inverse solution estimated a consumption for shrimp of 6.933 t km^{-2} yr^{-1} (Q/B = 19.541 yr^{-1}) and 15.645 t km^{-2} yr^{-1} (Q/B = 21.029 yr^{-1}) during the mid-1980s and mid-1990s, respectively.

Snow crab consumption data were obtained from a study conducted in the baie des Chaleurs and the southern Gulf of St. Lawrence (Brêthes et al. 1984). A daily ration of 0.4% of body mass was estimated, resulting in a Q/B ratio of 1.460 yr^{-1}. A second estimate was derived from a study of the physiological energetics of the snow crab (Thompson and Hawryluk 1990). The estimated Q/B ratio was 1.302 yr^{-1}. When the resulting minimum and maximum biomass values and the previous Q/B ratios were used for each period, we obtained consumption ranges of 3.873 to 4.370 and 3.032 to 4.961 t km^{-2} yr^{-1} during the mid-1980s and mid-1990s, respectively. Based on the mean production (0.841 and 0.944 t km^{-2} yr^{-1}) for each period and the minimum and maximum GE limits (10–30%), we obtained other consumption ranges of 2.805 to 8.414 and 3.146 to 9.437 t km^{-2} yr^{-1} during the mid-1980s and mid-1990s, respectively. Assuming that these species would eat at least as much food as their biomass ($Q/B \geq 1$), the resulting lower and upper consumption limits were 2.993 (instead of 2.805) to 8.414 t km^{-2} yr^{-1} and 3.032 to 9.437 t km^{-2} yr^{-1}, respectively, for the two periods. The inverse solution estimated a consumption of 3.986 t km^{-2} yr^{-1} (Q/B = 1.332 yr^{-1}) and 5.995 t km^{-2} yr^{-1} (Q/B = 2.093 yr^{-1}) for large crustaceans during the mid-1980s and mid-1990s, respectively.

Diet composition

Stomach content data for shrimp from NAFO division 4T were not available for the studied periods. Diet information for this group was taken from Bundy et al. (2000). Feeding occurs in both the benthic and pelagic environments, in accordance with their daily vertical migrations. Annelids, small crustaceans, detritus, and bottom plants were the main prey during the day while copepods and euphausiids were the principal prey items during the nocturnal migration. We used these diet data for the two periods (Table 13).

Stomach content data for snow crab were available from NAFO division 4T in 1999 (n = 1,048) (M. Hanson, unpublished data). The main prey of snow crab were detritus, molluscs, echinoderms, and crustaceans. We used these diet data for the two periods (Table 13).

Table 13. Diet compositions of shrimp and large crustacea used in modelling. Est: diet estimates by the inverse model; TRN: number of trophic relations; SD: standard deviation. All values are percentages except TRN. Groups with indicated CV (available only as point estimates): Min = mean – (mean x 50%), Max = mean + (mean x 50%). Empty cells indicate that a prey item was never found whereas "0.0" indicates that it was found in very small amounts. Values used in data equations or as upper and lower limit constraints are indicated in boldface.

	Shrimp (CV= 50%)					
Prey	Mean	± SD	Min	Max	Est. (mid-1980s)	Est. (mid-1990s)
Large cod						
Small cod						
Green. halibut						
Small Amer. plaice						
Large Amer. plaice						
Flounders						
Skates						
Redfish						
Large demersals						
Small demersals						
Capelin						
Large pelagics						
Pisci. small pelagics						
Plank. small pelagics						
Shrimp	**0.0**		0.0	0.0	0.0	0.0
Large crustacea						
Echinoderms						
Molluscs						
Polychaetes	1.5		**0.8**	**2.3**	1.6	1.6
Other bent. inver.	1.5		**0.8**	**2.3**	1.7	1.6
Large zooplankton	12.0		**6.0**	**18.0**	10.9	11.5
Small zooplankton	24.0		**12.0**	**36.0**	21.1	27.0
Phytoplankton	8.5		**4.3**	**12.8**	10.6	13.1
Detritus	52.5		**26.3**	**78.8**	54.1	45.2
Total	100.0		50.0	150.0	100.0	100.0
TRN	7					

Table 13. Cont.

	Large crustacea (mid-1980s) (CV= 60%)					Large crustacea (mid-1990s) (CV= 50%)				
Prey	Mean	± SD	Min	Max	Est	Mean	± SD	Min	Max	Est
Large cod										
Small cod										
Green. halibut										
Small Amer. plaice										
Large Amer. plaice										
Flounders										
Skates										
Redfish										
Large demersals										
Small demersals										
Capelin										
Large pelagics										
Pisci. small pelagics										
Plank. small pelagics										
Shrimp	3.8		**1.5**	**6.1**	2.4	3.8		**1.9**	**5.7**	3.3
Large crustacea	10.6		**4.2**	**16.9**	4.2	10.6		**5.3**	**15.9**	6.0
Echinoderms	15.2		**6.1**	**24.2**	16.7	15.2		**7.6**	**22.7**	14.1
Molluscs	20.8		**8.3**	**33.3**	26.7	20.8		**10.4**	**31.2**	25.1
Polychaetes	12.7		**5.1**	**20.3**	15.2	12.7		**6.4**	**19.1**	12.8
Other bent. inver.	4.0		**1.6**	**6.4**	4.5	4.0		**2.0**	**6.0**	4.2
Large zooplankton	1.8		**0.7**	**2.9**	2.1	1.8		**0.9**	**2.7**	2.1
Small zooplankton										
Phytoplankton										
Detritus	31.1		**12.4**	**49.8**	28.1	31.1		**15.6**	**46.7**	32.5
Total	100.0		40.0	160.0	100.0	100.0		50.0	150.0	100.0
TRN	8					8				

Benthic invertebrates

Background

The benthic invertebrates were divided into four groups: echinoderms, molluscs, polychaetes, and other benthic invertebrates. This last group consisted mainly of miscellaneous crustaceans, nematodes, and other meiofauna. Except for specific abundance values, there was very little information available on benthic data for the southern Gulf of St. Lawrence. Consequently, in many cases it was assumed that benthic biomass was similar to that of the Newfoundland–Labrador Shelf ecosystem (Bundy et al. 2000). The most recent comprehensive

source of information on the benthos is a study carried out in 1980 under the auspices of the Mobil Oil Company on the Grand Banks of Newfoundland (Hutcheson et al. 1981).

For all the molluscs considered in the ecosystem, only part of the biomass, the soft body tissue, is transferred through the food web. This is confirmed by observations of huge shell beds on the ocean floor (Hutcheson et al. 1981). In order to reduce the biomass and account for soft body tissue only, the ratio of the body mass to whole mass of the mollusc *Mesodesma deauratum* was estimated. The mean ratio between blotted wet mass of tissue to whole mass for animals with a shell length between 30 and 35 mm was 0.166 ± 0.023 (N = 10; K. Gilkinson, DFO, Northwest Atlantic Fisheries Centre, St. John's, Newfoundland, unpublished data).

Catch

Polychaetes, echinoderms, and other benthic invertebrates were not exploited commercially in the study area during the 1985–1987 and 1994–1996 periods. Only molluscs were commercially harvested. The most common large bivalve in cod stomachs is the northern propellor clam (*Cyrtodaria siliqua*), but it is not harvested commercially. Commercially harvested species include hard clams (*Mercenaria mercenaria*), sea scallops (*Placopecten magellanicus*), whelks (*Busycon* sp.), and Stimpson clam (*Spisula polynyma)*. Average annual landings were taken from the NAFO statistics and were 3,295 t or 5.14×10^{-2} t km^{-2} yr^{-1} and 4,513 t or 7.04×10^{-2} t km^{-2} yr^{-1}, respectively, for each of the two periods (NAFO 1999). Using the previous ratio (16.6%) of blotted wet mass of tissue to whole mass for animals, we corrected the previous landings estimated for the whole mass including the shell to landings for soft body tissue only. We obtained $8.54 \times 10^{-3} \pm 5.24 \times 10^{-4}$ and $1.17 \times 10^{-2} \pm 7.86 \times 10^{-4}$ t km^{-2} yr^{-1} during the mid-1980s and mid-1990s, respectively. The inverse solution estimated a catch value of 8.60×10^{-3} and 1.17×10^{-2} t km^{-2} yr^{-1}, respectively, for each of the two periods.

Biomass

The mean biomasses for 4T were assumed to be the same as for 2J3KLNO and were 112.300 t km^{-2} for echinoderms, 42.100 t km^{-2} for molluscs, 10.500 t km^{-2} for polychaetes, and 7.800 t km^{-2} for other benthic invertebrates in the two periods.

Production

There is no information available on production estimates of benthic invertebrates in the southern Gulf. All the estimates are taken from the literature for other areas.

Echinoderms

Warwick et al. (1978) estimated an annual production of 0.229 t km^{-2} yr^{-1} for echinoderms in Carmarthen Bay (South Wales, U.K.) while Buchanan and Warwick (1974) found an estimate of 0.108 t km^{-2} yr^{-1}. However, higher echinoderm productions have been reported in the New

York Bight (70.108 t km^{-2} yr^{-1}, Steimle 1985) and on Georges Bank (64.221 t km^{-2} yr^{-1}, Steimle 1987). Production could thus range between 0.108 and 70.108 t km^{-2} yr^{-1}, corresponding to an annual production of 33.667 ± 38.755 t km^{-2} yr^{-1}. We used these values for the two periods. The inverse solution estimated a production of 33.343 t km^{-2} yr^{-1} (P/B of 0.297 yr^{-1}) and 39.495 t km^{-2} yr^{-1} (P/B of 0.352 yr^{-1}) during the mid-1980s and mid-1990s, respectively.

Molluscs

For molluscs, Warwick et al. (1978) estimated an annual production of 3.824 t km^{-2} yr^{-1} in Carmarthen Bay (South Wales, U.K.) while Sanders (1956) estimated 4.671 t km^{-2} yr^{-1} in Long Island Sound. Higher production estimates were reported by Steimle (1985) (82.121 t km^{-2} yr^{-1}) and by Borkowski (1974) (23.530 t km^{-2} yr^{-1}), as well as lower estimates such as 0.600 t km^{-2} yr^{-1} in Buchanan and Warwick (1974). Production could thus range between 0.600 and 82.121 t km^{-2} yr^{-1}, corresponding to an annual production of 22.949 ± 34.282 t km^{-2} yr^{-1}. We used these values for the two periods. The inverse solution estimated a production of 49.108 t km^{-2} yr^{-1} (P/B of 1.166 yr^{-1}) and 44.024 t km^{-2} yr^{-1} (P/B of 1.046 yr^{-1}) during the mid-1980s and mid-1990s, respectively.

Polychaetes

Estimates of the annual production of polychaetes ranged between 0.206 and 74.564 t km^{-2} yr^{-1} (0.206 t km^{-2} yr^{-1} in Buchanan and Warwick [1974], 0.939 t km^{-2} yr^{-1} in Warwick et al. [1978], 5.522 t km^{-2} yr^{-1} in Sanders [1956], 6.310 t km^{-2} yr^{-1} in Collie [1987], 8.250 t km^{-2} yr^{-1} in Peer [1970], 16.050 t km^{-2} yr^{-1} in Nichols [1975], 21.600 t km^{-2} yr^{-1} in Curtis [1977], and 74.564 t km^{-2} yr^{-1} in Steimle [1985]). This represented an annual production of 16.680 ± 27.487 t km^{-2} yr^{-1} for the two periods. The inverse solution estimated a production of 30.808 t km^{-2} yr^{-1} (P/B of 2.934 yr^{-1}) and 31.119 t km^{-2} yr^{-1} (P/B of 2.964 yr^{-1}) during the mid-1980s and mid-1990s, respectively.

Other benthic invertebrates

Estimates of annual production for other benthic invertebrates ranged between 0.517 and 15.677 t km^{-2} yr^{-1} (0.517 t km^{-2} yr^{-1} in Sheader [1977], 5.000 t km^{-2} yr^{-1} in Klein et al. [1975], 15.500 t km^{-2} yr^{-1} in Cederwall [1977], and 15.677 t km^{-2} yr^{-1} in Collie [1985]). This represented an annual production of 9.173 ± 7.631 t km^{-2} yr^{-1} for the two periods. The inverse solution estimated a production of 9.425 t km^{-2} yr^{-1} (P/B of 1.208 yr^{-1}) and 8.955 t km^{-2} yr^{-1} (P/B of 1.148 yr^{-1}) during the mid-1980s and mid-1990s, respectively.

Consumption

In the absence of information on food consumption, consumption values were estimated by taking gross growth efficiency (GE) between 0.09 and 0.30 (Christensen and Pauly 1992). For echinoderms, this produced a consumption range between 112.222 and 374.072 t km^{-2} yr^{-1}, corresponding to a mean consumption of 243.147 ± 185.156 t km^{-2} yr^{-1}. We used these values for the two periods. The modelling consumption estimate was 145.205 t km^{-2} yr^{-1} (Q/B of 1.293 yr^{-1}) and 174.811 t km^{-2} yr^{-1} (Q/B of 1.557 yr^{-1}) during the mid-1980s and mid-1990s, respectively.

For molluscs, this produced a consumption range between 76.497 and 254.991 t km^{-2} yr^{-1}, corresponding to a mean consumption of 165.744 ± 126.214 t km^{-2} yr^{-1}. We used these values for the two periods. The modelling consumption estimate was 180.390 t km^{-2} yr^{-1} (Q/B of 4.285 yr^{-1}) and 185.903 t km^{-2} yr^{-1} (Q/B of 4.416 yr^{-1}) during the mid-1980s and mid-1990s, respectively.

For polychaetes, this produced a consumption range between 55.601 and 185.336 t km^{-2} yr^{-1}, corresponding to a mean consumption of 120.468 ± 91.737 t km^{-2} yr^{-1}. We used these values for the two periods. The modelling consumption estimate was 119.932 t km^{-2} yr^{-1} (Q/B of 11.422 yr^{-1}) and 139.087 t km^{-2} yr^{-1} (Q/B of 13.246 yr^{-1}) during the mid-1980s and mid-1990s, respectively.

For other benthic invertebrates, this produced a consumption range between 30.578 and 101.926 t km^{-2} yr^{-1}, corresponding to a mean consumption of 66.252 ± 50.451 t km^{-2} yr^{-1}. We used these values for the two periods. The modelling consumption estimate was 47.813 t km^{-2} yr^{-1} (Q/B of 6.130 yr^{-1}) and 55.838 t km^{-2} yr^{-1} (Q/B of 7.159 yr^{-1}) during the mid-1980s and mid-1990s, respectively.

Diet composition

For echinoderms, diet information was taken from the three most abundant species in NAFO divisions 2J3KL: the sand dollar (*Echinarchnius parma*), the sea urchin (*Strongylocentrotus pallidus*), and the brittle star (*Ophiura robusta*). The resulting diet is 100% detritus (Bundy et al. 2000).

For molluscs, Bundy et al. (2000) analyzed the diet composition of a suspension feeder (*Macoma deauratum*), a deposit feeder (*Macoma calcarea*), and a suspension or detrital feeder (*Liocyma fluctuosa*). Suspension feeders feed on organic detrital matter that is resuspended in the water immediately above the sediment surface. Deposit feeders can be considered as detrital feeders. Thus, the molluscs are assumed to be detrital feeders of various forms and the diet of the mollusc group is 100% detritus. However, in shallower waters, molluscs could consume phytoplankton (M. Fréchette, DFO, Institut Maurice-Lamontagne, Mont-Joli, Québec, personal communication). This potential food was also accounted for in the final diet composition for the two periods (Table 14).

The polychaetes are considered to have a diet of 100% detritus (Nesis 1965; Fauchald and Jumars 1979). However, recent studies in the Gulf of St. Lawrence showed that polychaetes could also consume phytoplankton and that cannibalism could have a significant impact in the diet composition (Desrosiers et al. 2000). The resulting diet used for the two periods is shown in Table 14.

The key organisms for the other benthic invertebrates group are gammarid amphipods. These species feed mainly on organic detritus (Nesis 1965; Hutcheson et al. 1981).

Table 14. Diet compositions of molluscs and polychaetes used in modelling. Est: diet estimates by the inverse model; TRN: number of trophic relations; SD: standard deviation. All values are percentages except TRN. Groups with indicated CV (available only as point estimates): Min = mean – (mean x 50%), Max = mean + (mean x 50%). Empty cells indicate that a prey item was never found whereas "0.0" indicates that it was found in very small amounts. Values used in data equations or as upper and lower limit constraints are indicated in boldface.

	Molluscs					
Prey	Mean	± SD	Min	Max	Est. (mid-1980s)	Est. (mid-1990s)
Large cod						
Small cod						
Green. halibut						
Small Amer. plaice						
Large Amer. plaice						
Flounders						
Skates						
Redfish						
Large demersals						
Small demersals						
Capelin						
Large pelagics						
Pisci. small pelagics						
Plank. small pelagics						
Shrimp						
Large crustacea						
Echinoderms						
Molluscs						
Polychaetes						
Other bent. inver.						
Large zooplankton						
Small zooplankton						
Phytoplankton	50.0	35.4	**50.0**	**100.0**	50.0	50.0
Detritus	50.0	35.4	**50.0**	**100.0**	50.0	50.0
Total	100.0		100.0	200.0	100.0	100.0
TRN	2					

Table 14. Cont.

	Polychaetes (CV= 50%)					
Prey	Mean	± SD	Min	Max	Est. (mid-1980s)	Est. (mid-1990s)
Large cod						
Small cod						
Green. halibut						
Small Amer. plaice						
Large Amer. plaice						
Flounders						
Skates						
Redfish						
Large demersals						
Small demersals						
Capelin						
Large pelagics						
Pisci. small pelagics						
Plank. small pelagics						
Shrimp						
Large crustacea						
Echinoderms						
Molluscs						
Polychaetes	26.0		**13.0**	**38.9**	18.6	16.4
Other bent. inver.						
Large zooplankton						
Small zooplankton						
Phytoplankton	37.0		**18.5**	**55.5**	51.6	50.4
Detritus	37.0		**18.5**	**55.5**	29.8	33.2
Total	100.0		50.0	150.0	100.0	100.0
TRN	3					

Large zooplankton

Background

Species representing this group are greater than 5 mm in length and include euphausiids, chaetognaths, hyperiid amphipods, jellyfish (cnidarians and ctenophores), mysids, tunicates, and ichthyoplankton. This group contains herbivorous (some euphausiid species), omnivorous (most euphausiids, hyperid amphipods, mysiids, and large tunicates), and carnivorous (chaetognaths and jellyfish) species.

Catch

There was no commercial fishery for species in this group during the two periods in the southern Gulf.

Biomass

The biomass of large zooplankton was calculated from an annual survey of stage I egg production of Atlantic mackerel conducted in June/early July in the southern Gulf of St. Lawrence from 1982 to 1991 (Runge et al. 1999). Even though that study referred to organisms greater than 1 mm in length, which included both small and large zooplankton, we used their biomass estimate as a guesstimate in the absence of more current information. A factor of 5 was used to convert dry matter to wet matter (Harris et al. 2000). This resulted in a biomass estimate of 5.750 ± 2.636 t km^{-2} during the mid-1980s and 8.750 ± 1.250 t km^{-2} in 1991, which was used for the mid-1990s.

Production

The euphausiid production estimate was obtained from several different sources. These sources included P/B ratios of 4.000 yr^{-1} for the Gulf of St. Lawrence (Berkes 1977), 2.750 yr^{-1} (range: 1.300–4.200 yr^{-1}; Lindley 1980) to 3.840 yr^{-1} (range: 1.300–6.300 yr^{-1}; Lindley 1982) for the North Sea, and 1.600 yr^{-1} for the northeast Atlantic off the west coast of Ireland (Mauchline 1985). When the minimum and maximum biomass values were used for each period, we obtained a production range of 4.640 to 32.400 and 12.000 to 40.000 t km^{-2} yr^{-1}, respectively, for each of the two periods. The modelling production estimate was 24.570 t km^{-2} yr^{-1} (P/B = 4.273 yr^{-1}) and 33.516 t km^{-2} yr^{-1} (P/B = 3.830 yr^{-1}) during the mid-1980s and mid-1990s, respectively.

Consumption

Consumption was estimated from data on euphausiids in the Gulf of St. Lawrence (Sameoto 1976). This produced a consumption range between 46.370 and 207.938 t km^{-2} yr^{-1}. Based on the mean production (18.520 and 26.000 t km^{-2} yr^{-1}) for each period and the minimum and maximum GE limits (10–30%), we obtained another consumption range of 61.733 to 185.200 t km^{-2} yr^{-1} and 86.667 to 260.000 t km^{-2} yr^{-1}, respectively, for each of the two periods. The resulting lower and upper consumption limits were 46.370 and 207.938 t km^{-2} yr^{-1} and 46.370 and 260.000 t km^{-2} yr^{-1}, respectively, for each of the two periods. The modelling consumption estimate was 170.006 t km^{-2} yr^{-1} (Q/B = 29.566 yr^{-1}) and 210.505 t km^{-2} yr^{-1} (Q/B = 24.058 yr^{-1}) during the mid-1980s and mid-1990s, respectively.

Diet composition

No diet information was available for these species in the southern Gulf of St. Lawrence. In other areas, euphausiids feed on detritus, phytoplankton, chaetognaths, amphipods, and crustaceans (copepods) (Mauchline 1980). Chaetognaths and jellyfish eat copepods (Sullivan 1980; Smayda 1993). The relative proportions of these prey in the resulting large zooplankton diet were 5% large zooplankton, 43% small zooplankton, 37% phytoplankton, and 15% detritus (Bundy et al. 2000) (Table 15).

Table 15. Diet composition of large zooplankton used in modelling for each period. Est: diet estimates by the inverse model; TRN: number of trophic relations; SD: standard deviation. All values are percentages except TRN. Empty cells indicate that a prey item was never found whereas "0.0" indicates that it was found in very small amounts. Values used in data equations or as upper and lower limit constraints are indicated in boldface.

	Large zooplankton (> 5 mm)					
Prey	Mean	± SD	Min	Max	Est. (mid-1980s)	Est. (mid-1990s)
Large cod						
Small cod						
Green. halibut						
Small Amer. plaice						
Large Amer. plaice						
Flounders						
Skates						
Redfish						
Large demersals						
Small demersals						
Capelin						
Large pelagics						
Pisci. small pelagics						
Plank. small pelagics						
Shrimp						
Large crustacea						
Echinoderms						
Molluscs						
Polychaetes						
Other bent. inver.						
Large zooplankton	5.0	6.9	**0.0**	**11.9**	0.6	2.5
Small zooplankton	43.0	7.1	**38.0**	**48.0**	38.0	38.8
Phytoplankton	37.0	29.4	**0.0**	**66.4**	51.4	48.3
Detritus	15.0	7.1	**10.0**	**20.0**	10.0	10.3
Total	100.0		48.0	146.3	100.0	100.0
TRN	4					

Small zooplankton

Background

The small zooplankton includes zooplankton less than or equal to 5 mm in length. Copepods, mainly *Oithona similis*, *Temora longicornis*, *Pseudocalanus* spp., and *Calanus finmarchicus*, are the most numerous small plankton. Also included in the small zooplankton category were meroplankton and tunicates < 5 mm, which are generally underestimated by sampling gear, as well as heterotrophic protozoa (flagellates, dinoflagellates, and ciliates) (Strong 1981). The most recent comprehensive source of information on the small zooplankton in the Gulf of St. Lawrence was a study carried out from July 1992 to June 1994 during the Canadian Joint Global Ocean Flux Study (JGOFS) program (Roy et al. 2000). The small cyclopoid copepod *Oithona similis* was very abundant, ranging from 20 to 70% of the numerical abundance of all species.

Catch

None.

Biomass

Zooplankton was sampled around mid-day and mid-night, using a WP-2 net (mesh size = 200 µm) (Roy et al. 2000). Data from these day and night hauls were averaged over the whole water column (top 50–75 m) for each season (Savenkoff et al. 2000). The mean biomass for the entire area was 4,047 ± 2,603 mg C m^{-2} for all the small zooplankton. The range was wide and we assumed that it should account for the heterotrophic protozoan (flagellates, dinoflagellates, and ciliates) biomass (1,080 ± 788 mg C m^{-2}). Using a conversion factor of 10 g wet mass equal to 1g C (Christensen and Pauly 1992), we obtained 40.469 ± 26.032 t wet mass km^{-2}. The minimum and maximum range was 14.436 to 66.501 t wet mass km^{-2}. Based on de Lafontaine et al. (1991; see their Fig. 7), another minimum–maximum biomass range was estimated as 1–24 g dry mass m^{-2} or 5.000–120.000 t wet mass km^{-2} yr^{-1} for small zooplankton. The resulting biomass could thus range between 5.000 and 120.000 t km^{-2}, corresponding to a mean value of 50.000 ± 81.317 t km^{-2} for the two periods.

Production

Production (94.76 mg C m^{-2} d^{-1} or 345.886 t wet mass km^{-2} yr^{-1}) was estimated in the Gulf of St. Lawrence from Vézina et al. (2000). However, de Lafontaine et al. (1991) estimated 1 g C m^{-2} mo^{-1} (or 120.00 t wet mass km^{-2} yr^{-1}) for secondary production of copepod-sized organisms. Production could thus range between 120.000 and 345.886 t km^{-2} yr^{-1}, corresponding to an annual production of 232.943 ± 159.725 t km^{-2} yr^{-1} for the two periods. The modelling production

estimate was 321.192 t km^{-2} yr^{-1} (P/B = 6.424 yr^{-1}) and 331.510 t km^{-2} yr^{-1} (P/B = 6.630 yr^{-1}) during the mid-1980s and mid-1990s, respectively.

Consumption

Vézina et al. (2000) estimated a minimum consumption value (120.04 mg C m^{-2} d^{-1} or 438.135 t wet mass km^{-2} yr^{-1}) for the summer and fall periods and a maximum (425.94 mg C m^{-2} d^{-1} or 1,554.666 t wet mass km^{-2} yr^{-1}) value for the winter and spring periods. These lower and upper limits, along with the corresponding mean (272.99 ± 216.30 mg C m^{-2} d^{-1} or 996.401 ± 789.507 t wet mass km^{-2} yr^{-1}) were used for the two periods. The modelling consumption estimate was 1,138.283 t km^{-2} yr^{-1} (Q/B = 22.766 yr^{-1}) and 1,218.645 t km^{-2} yr^{-1} (Q/B = 24.373 yr^{-1}) during the mid-1980s and mid-1990s, respectively.

Diet composition

The small zooplankton feed on both autotrophic and heterotrophic microplankton. However, heterotrophic microplankton (heterotrophic dinoflagellates, ciliates, and small metazoans) were included in the small zooplankton group here. Moreover, there is ample empirical evidence that mesozooplankton are omnivorous (Stoecker and Capuzzo 1990; Ohman and Runge 1994; Vézina et al. 2000). Small zooplankton, phytoplankton, and detritus were thus assumed to be potentially accessible to small zooplankton. We used the same resulting diet composition for small zooplankton for the two periods (Table 16).

Table 16. Diet composition of small zooplankton used in modelling for each period. Est: diet estimates by the inverse model; TRN: number of trophic relations; SD: standard deviation. All values are percentages except TRN. Empty cells indicate that a prey item was never found whereas "0.0" indicates that it was found in very small amounts. Values used in data equations or as upper and lower limit constraints are indicated in boldface.

	Small zooplankton (< 5 mm)					
Prey	Mean	± SD	Min	Max	Est. (mid-1980s)	Est. (mid-1990s)
Large cod						
Small cod						
Green. halibut						
Small Amer. plaice						
Large Amer. plaice						
Flounders						
Skates						
Redfish						
Large demersals						
Small demersals						
Capelin						
Large pelagics						
Pisci. small pelagics						
Plank. small pelagics						
Shrimp						
Large crustacea						
Echinoderms						
Molluscs						
Polychaetes						
Other bent. inver.						
Large zooplankton						
Small zooplankton	12.5	12.5	**9.3**	**26.9**	10.3	11.8
Phytoplankton	54.1	47.6	**0.0**	**67.3**	65.1	54.6
Detritus	33.4	35.2	**23.4**	**73.1**	24.5	33.7
Total	100.0		32.7	167.3	100.0	100.0
TRN	3					

Phytoplankton

Background

Most information on phytoplankton in the Gulf of St. Lawrence was derived from a study carried out from July 1992 to June 1994 during the Canadian Joint Global Ocean Flux Study (JGOFS) program (Savenkoff et al. 2000). These authors described the seasonal changes in photosynthetic production, respiration, sinking flux of organic carbon, and food web structure in the Gulf of St. Lawrence over a two-year period.

Diatoms were the most abundant phytoplankton in terms of both cell numbers and biovolumes during spring and winter. A mixture of autotrophic and mixotrophic organisms including cryptophytes, diatoms, dinoflagellates, prasinophytes, and mixotrophic *Stombidium* spp. (in the Spirotrichea) dominated during summer and fall. Prymnesiophytes were important in terms of cell numbers during spring and winter. The diatoms were dominated by *Chaetoceros affinis*, *Chaetoceros* spp., *Leptocylindrus minimus*, and *Thalassiosira nordenskioldii* during winter and by *Thalassiosira* spp. (*T. punctigera*, *T. nordenskioldii*, *T. pacifica*, and *T. bioculata*) and *Fragilariopsis* spp. (*F. oceanica* and *F. cylindrus*) during spring. During summer, the importance of diatoms in the phytoplankton composition was lower, with the majority observed being smaller centric diatoms such as *Minidiscus* sp., *Chaetoceros minimus*, and occasionally larger *Coscinodiscus* sp.

Phytoplankton biomass and production were the only two parameters required for modelling. There was no harvest, and since they are autotrophs, there is no consumption or diet.

Biomass

Phytoplankton biomass is measured as chlorophyll *a* biomass. Mean annual chlorophyll *a* biomass (21 ± 11 mg CHL m^{-2}) was estimated as the mean of the seasonal biomass averages integrated over the euphotic zone (defined as the depth of 1% surface incident radiation) (Savenkoff et al. 2000). To facilitate comparisons with other studies in the Gulf of St. Lawrence, phytoplankton carbon biomass was estimated by converting measured chlorophyll *a* concentrations (CHL) to carbon (C) using a C/CHL ratio of 50 (Rivkin et al. 1996; Savenkoff et al. 2000).

The mean biomass for the entire area was 1.9 ± 1.2 g C m^{-2} or 18.035 ± 8.763 t km^{-2}, using a conversion factor of 10 g wet mass equal to 1g C (Christensen and Pauly 1992). The minimum–maximum range was of 4.885 to 63.954 t km^{-2}. We used these values for the two periods.

Primary production or phytoplankton production

Primary production was estimated from the same data sources as described above. After correcting for phytoplankton respiration (64 ± 208 mg C m^{-2} d^{-1}), a value of 483 ± 214 mg C m^{-2} d^{-1} was estimated over the euphotic zone (Savenkoff et al. 2000). This represented 176.38 ± 78.09 g C m^{-2} yr^{-1} or 1,763.773 ± 780.945 t km^{-2} yr^{-1}. The minimum and maximum range was 982.828 to 2,544.718 t wet mass km^{-2} yr^{-1}. We used these values for the two periods. The modelling

production estimate was 1,307.722 t km^{-2} yr^{-1} (P/B = 72.509 yr^{-1}) and 1,548.319 t km^{-2} yr^{-1} (P/B = 85.849 yr^{-1}) during the mid-1980s and mid-1990s, respectively.

Detritus

Biomass

The detritus mass was estimated using an empirical relationship derived by Pauly et al. (1993) that relates detritus biomass to primary productivity and euphotic depth.

$$\log_{10} D = -2.41 + 0.954 \log_{10} PP + 0.863 \log_{10} E \quad (8)$$

where D is the standing stock of detritus (g C m^{-2}), PP is primary productivity (g C m^{-2} yr^{-1}), and E is the euphotic depth (m).

The annual value for primary production was 199.8 ± 77.8 g C m^{-2} yr^{-1}. The euphotic depth was estimated from Savenkoff et al. (2000) as 23.5 ± 6.0 m. The primary production estimate and euphotic depth were substituted into equation 8, giving a range of detritus biomass estimates from 4.5 to 15.5 g C m^{-2}, or 45.014 to 154.950 t km^{-2}, using a conversion factor of 10 g wet mass equal to 1g C (Christensen and Pauly 1992). This resulted in a mean detritus biomass of 93.008 ± 77.737 t km^{-2}. We used these values for the two periods.

Here, bacteria was considered part of the detritus compartment. Detritus estimates had a wide range, and it was assumed that this range should allow for the bacteria biomass (bacterial biomass: 163 ± 36 mg C m^{-2} or 1.626 ± 0.357 t km^{-2}; Savenkoff et al. 2000).

Respiration

Detritus is usually assumed not to respire. However, as bacteria were considered part of the detritus in this study, there would be respiration involved. Based on Savenkoff et al. (2000), we estimated a planktonic respiration (organisms < 200 µm including bacteria) close to 174 ± 51 mg C m^{-2} d^{-1} and 404 ± 190 mg C m^{-2} d^{-1} for the winter–spring and summer–fall periods, respectively, in the euphotic zone of the southern Gulf of St. Lawrence. Vézina et al. (2000) applied inverse modelling to the data collected from July 1992 to June 1994 to estimate trophic flows in the planktonic food web and to calculate export fluxes consistent with mass balance. These authors estimated that the phytoplankton respiration represented 8 and 20% of the primary production for the winter–spring and summer–fall periods, respectively (R_{PHY} = 60 ± 33 mg C m^{-2} d^{-1} for winter–spring and 68 ± 21 mg C m^{-2} d^{-1} for summer–fall). By subtracting, we could estimate a detrital (or bacterial) respiration of 114 ± 60 mg C m^{-2} d^{-1} and 336 ± 191 mg C m^{-2} d^{-1} for the winter–spring and summer–fall periods, respectively. This represented 225 ± 100 mg C m^{-2} d^{-1} or 82.0 ± 36.5 g C m^{-2} yr^{-1} for the euphotic zone.

Based on the data collected from July 1992 to June 1994 at two stations located in the southern Gulf, Savenkoff et al. (2000) estimated a bacterial respiration of 16 ± 15 mg C m^{-2} d^{-1} or 6 ± 5 g C m^{-2} yr^{-1} in the aphotic layer. By adding bacterial respiration values estimated in the euphotic and aphotic layers, a total detrital respiration could be estimated as 87.9 ± 36.9 g C m^{-2}

yr^{-1} or 878.750 ± 369.066 t km^{-2} yr^{-1} (range: 509.684–1,247.815 t km^{-2} yr^{-1}) for the two periods. The inverse solution estimated a detrital respiration of 530.690 and 629.673 t km^{-2} yr^{-1} during the mid-1980s and mid-1990s, respectively.

Export

The fraction of the organic carbon that is not returned to the water column but is buried and preserved within the sediment represents the export of detritus. Silverberg et al. (2000) estimated a burial flux of particulate organic carbon between 0.46 and 0.53 mol C m^{-2} yr^{-1} in the Gulf of St. Lawrence. This represented a detrital export close to 5.9 ± 0.6 g C m^{-2} yr^{-1} or 5.94 x 10^1 ± 0.59 x 10^1 t km^{-2} yr^{-1}. The inverse solution estimated a detrital export of 5.46 x 10^1 and 5.42 x 10^1 t km^{-2} yr^{-1} during the mid-1980s and mid-1990s, respectively.

Data synthesis

Data about biomass, export (here equal to commercial catch), production, and consumption are summarized in Tables 17 to 20 for each period.

Table 17. Observed biomass and export for each group used as input parameters for modelling for the 1985–1987 period in the southern Gulf of St. Lawrence. SD: standard deviation, Min: minimum, Max: maximum. Est: value estimates by inverse modelling. Values used in data equations or as upper and lower limit constraints are indicated in boldface.

	Biomass (t wet mass km^{-2})				Export (t km^{-2} yr^{-1})[a]				
Group	Value	± SD	Min	Max	Value	± SD	Min	Max	Est.
Cetaceans	0.024	0.001	0.02	0.02	**3.75×10^{-4}**	2.09×10^{-5}	3.60×10^{-4}	3.90×10^{-4}	3.71×10^{-4}
Harp seals	0.231	0.013	0.22	0.24	6.39×10^{-4}	3.80×10^{-4}	**3.70×10^{-4}**	**9.07×10^{-4}**	6.52×10^{-4}
Hooded seals	0.003	0.000	0.003	0.003					
Grey seals	0.028	0.002	0.026	0.030	**7.17×10^{-4}**	6.96×10^{-4}	1.45×10^{-4}	1.68×10^{-3}	9.06×10^{-4}
Harbour seals	0.001	0.000	0.001	0.001					
Seabirds	0.004	0.002[b]			**3.35×10^{-4}**	1.69×10^{-4}[c]			2.76×10^{-4}
Large cod	5.248	0.956	4.152	5.906	9.72×10^{-1}	1.11×10^{-1}	8.51×10^{-1}	**1.07**	1.10
Small cod	1.247	0.322	1.002	1.612					
Green. halibut	0.009	0.004	0.006	0.013	7.13×10^{-3}	3.42×10^{-3}	**3.28×10^{-3}**	**9.82×10^{-3}**	3.28×10^{-3}
Small Amer. plaice	4.802	0.836	3.849	5.415					
Large Amer. plaice	0.549	0.099	0.437	0.623	**1.30×10^{-1}**	*1.66×10^{-2}*	*1.15×10^{-1}*	*1.48×10^{-1}*	*1.31×10^{-1}*
Flounders	1.561	0.447	1.222	2.068	**4.62×10^{-2}**	1.02×10^{-2}	3.44×10^{-2}	5.22×10^{-2}	4.55×10^{-2}
Skates	0.080	0.013	0.070	0.094	**1.43×10^{-5}**	2.48×10^{-5}	0	4.30×10^{-5}	1.81×10^{-5}
Redfish	0.028	0.021	0.004	0.043	**2.14×10^{-3}**	9.16×10^{-4}	1.48×10^{-3}	3.19×10^{-3}	2.53×10^{-3}
Large demersals	0.343	0.111	0.217	0.426	**7.03×10^{-2}**	1.27×10^{-2}	6.15×10^{-2}	8.49×10^{-2}	6.63×10^{-2}
Small demersals	0.875	1.152	0.061	1.690					
Capelin	0.489	0.690	0.000	0.976	**2.89×10^{-3}**	4.12×10^{-3}	1.17×10^{-5}	7.62×10^{-3}	2.86×10^{-3}

Table 17. Cont.

	Biomass (t wet mass km^{-2})				Export (t km^{-2} yr^{-1})[a]				
Group	Value	± SD	Min	Max	Value	± SD	Min	Max	Est.
Large pelagics	0.028	0.010	0.018	0.037	**2.45×10^{-3}**	2.47×10^{-3}	6.71×10^{-5}	5.00×10^{-3}	2.42×10^{-3}
Pisci. small pel. feeders	4.933	1.700	3.363	6.738	**1.42×10^{-1}**	3.86×10^{-2}	1.12×10^{-1}	1.86×10^{-1}	1.29×10^{-1}
Plank. small pel. feeders	9.755	1.816	8.584	11.847	**1.02**	3.18×10^{-1}	6.96×10^{-1}	1.33	9.57×10^{-1}
Shrimp	0.355	0.501	0.000	0.709	**2.33×10^{-3}**	1.49×10^{-3}	7.74×10^{-4}	3.75×10^{-3}	2.11×10^{-3}
Large crustaceans	2.993	0.498	2.653	3.357	**3.88×10^{-1}**	1.24×10^{-1}	2.46×10^{-1}	4.73×10^{-1}	3.48×10^{-1}
Echinoderms	112.300	63.418[b]							
Molluscs	42.100	23.775[b]			**8.54×10^{-3}**	5.24×10^{-4}	7.99×10^{-3}	9.03×10^{-3}	8.60×10^{-3}
Polychaetes	10.500	5.930[b]							
Other benthic invertebrates	7.800	4.405[b]							
Large zooplankton	5.750	2.636	2.900	8.100					
Small zooplankton	50.000	81.317	5.000	120.000					
Phytoplankton	18.035	8.763	4.885	63.954					
Detritus	93.008	77.737	45.014	154.950	5.94×10^{1}	0.59×10^{1}	**5.35×10^{1}**	**6.53×10^{1}**	5.46×10^{1}

[a]: Export was mainly the catch (including landings and anthropogenic mortality as hunting, etc.). For detritus, export was loss of detritus buried as sediment.

[b]: calculated as $B_X * CV(B_Y)_{mean}$ with $CV(B_Y)_{mean} = 56\%$, the average of all coefficients of variation for observed biomass.

[c]: calculated as $Exp_X * CV(Exp_Y)_{mean}$ with $CV(Exp_Y)_{mean} = 50\%$, the average of all coefficients of variation for observed export.

Table 18. Observed biomass and export for each group used as input parameters for modelling for the 1994–1996 period in the southern Gulf of St. Lawrence. SD: standard deviation, Min: minimum, Max: maximum. Est: value estimates by inverse modelling. Values used in data equations or as upper and lower limit constraints are indicated in boldface.

	Biomass (t wet mass km^{-2})				Export (t km^{-2} yr^{-1})[a]				
Group	Value	± SD	Min	Max	Value	± SD	Min	Max	Est.
Cetaceans	0.034	0.001	0.033	0.036	**3.75×10^{-4}**	2.09×10^{-5}	3.60×10^{-4}	3.90×10^{-4}	3.78×10^{-4}
Harp seals	0.347	0.013	0.335	0.360	**4.91×10^{-3}**	6.48×10^{-3}	5.01×10^{-4}	1.23×10^{-2}	5.60×10^{-3}
Hooded seals	0.004	0.000	0.004	0.004					
Grey seals	0.052	0.002	0.049	0.054	**2.46×10^{-4}**	2.59×10^{-4}	5.95×10^{-5}	5.41×10^{-4}	2.44×10^{-4}
Harbour seals	0.002	0.000	0.002	0.002					
Seabirds	0.004	0.002[b]			**3.35×10^{-4}**	2.01×10^{-4}[c]			3.23×10^{-4}
Large cod	1.609	0.237	1.399	1.866	1.80×10^{-2}	2.39×10^{-3}	1.60×10^{-2}	**3.10×10^{-2}**	3.05×10^{-2}
Small cod	0.299	0.017	0.281	0.315					
Green. halibut	0.007	0.001	0.006	0.008	**1.92×10^{-3}**	1.13×10^{-3}	7.89×10^{-4}	3.05×10^{-3}	1.91×10^{-3}
Small Amer. plaice	3.815	0.606	3.356	4.502					
Large Amer. plaice	0.261	0.032	0.230	0.295	**3.22×10^{-2}**	9.07×10^{-3}	2.17×10^{-2}	3.76×10^{-2}	3.42×10^{-2}
Flounders	1.657	0.407	1.342	2.117	**2.09×10^{-2}**	3.68×10^{-3}	1.70×10^{-2}	2.43×10^{-2}	2.10×10^{-2}
Skates	0.040	0.006	0.035	0.046	**4.19×10^{-4}**	2.09×10^{-4}	2.20×10^{-4}	6.37×10^{-4}	3.80×10^{-4}
Redfish	0.019	0.019	0.007	0.033	**9.78×10^{-4}**	1.66×10^{-3}	1.82×10^{-5}	2.90×10^{-3}	1.07×10^{-3}
Large demersals	0.218	0.241	0.056	0.397	5.97×10^{-3}	8.09×10^{-3}	**8.73×10^{-4}**	**1.53×10^{-2}**	1.69×10^{-3}
Small demersals	0.304	0.270	0.114	0.495	**5.19×10^{-6}**	8.99×10^{-6}	0	1.56×10^{-5}	7.21×10^{-6}
Capelin	21.528	23.787	5.108	48.807	**1.91×10^{-3}**	1.07×10^{-3}	6.80×10^{-4}	2.63×10^{-3}	1.72×10^{-3}

Table 18. Cont.

	Biomass (t wet mass km^{-2})				Export (t km^{-2} yr^{-1})[a]				
Group	Value	± SD	Min	Max	Value	± SD	Min	Max	Est.
Large pelagics	0.140	0.088	0.065	0.237	**9.76×10^{-3}**	4.85×10^{-2}	5.53×10^{-3}	1.51×10^{-2}	1.04×10^{-2}
Pisci. small pel. feeders	1.157	0.895	0.524	1.790	**1.44×10^{-1}**	2.34×10^{-2}	1.18×10^{-1}	1.64×10^{-1}	1.46×10^{-1}
Plank. small pel. feeders	7.421	0.152	7.287	7.586	**1.36**	1.22×10^{-1}	1.23	1.46	1.36
Shrimp	0.744	1.028	0.026	1.479	**6.58×10^{-3}**	6.09×10^{-3}	1.32×10^{-3}	1.33×10^{-2}	6.62×10^{-3}
Large crustaceans	2.864	0.756	2.329	3.398	**3.71×10^{-1}**	4.68×10^{-2}	3.17×10^{-1}	4.01×10^{-1}	3.67×10^{-1}
Echinoderms	112.300	63.273[b]							
Molluscs	42.100	23.720[b]			**1.17×10^{-2}**	7.86×10^{-4}	1.10×10^{-2}	1.25×10^{-2}	1.17×10^{-2}
Polychaetes	10.500	5.916[b]							
Other benthic invertebrates	7.800	4.395[b]							
Large zooplankton	8.750	1.250	7.500	10.000					
Small zooplankton	50.000	81.317	5.000	120.000					
Phytoplankton	18.035	8.763	4.885	63.954					
Detritus	93.008	77.737	45.014	154.950	5.94×10^{1}	0.59×10^{1}	**5.35×10^{1}**	**6.53×10^{1}**	5.42×10^{1}

[a]: Export was mainly the catch (including landings and anthropogenic mortality as hunting, etc.). For detritus, export was loss of detritus buried as sediment.
[b]: calculated as $B_X * CV(B_Y)_{mean}$ with $CV(B_Y)_{mean} = 56\%$, the average of all coefficients of variation for observed biomass.
[c]: calculated as $Exp_X * CV(Exp_Y)_{mean}$ with $CV(Exp_Y)_{mean} = 60\%$, the average of all coefficients of variation for observed export.

Table 19. Observed production and consumption used as input parameters for modelling for the 1985–1987 period in the southern Gulf of St. Lawrence. SD: standard deviation, Min: minimum, Max: maximum. Est: value estimates by inverse modelling. Values used in data equations or as upper and lower limit constraints are indicated in boldface. Means and SDs were calculated on the two extreme values.

	Production (t km^{-2} yr^{-1})					Consumption (t km^{-2} yr^{-1})				
Group	Mean	± SD	Min	Max	Est.	Mean	± SD	Min	Max	Est.
Cetaceans	**0.0021**	0.002[a]			0.0014	0.236	0.030	**0.215**	**0.257**	0.219
Harp seals	0.019	0.016	**0.007**	**0.031**	0.016	1.888	1.649	**0.722**	**3.054**	2.030
Hooded seals	0.0002	0.0001	**0.0002**	**0.0003**	0.0003	0.033	0.004	**0.030**	**0.036**	0.030
Grey seals	0.0039	0.0032	**0.0017**	**0.0062**	0.0047	0.364	0.359	**0.110**	**0.618**	0.508
Harbour seals	0.00015	0.00015	**0.00005**	**0.00026**	0.00008	0.015	0.015	**0.005**	**0.026**	0.008
Seabirds	**0.0011**	0.0009[a]			0.0011	0.309	0.280	**0.111**	**0.507**	0.177
Large cod	2.817	0.514	**2.427**	**3.153**	2.434	18.162	14.155	**8.153**	**28.171**	8.231
Small cod	0.656	0.241	**0.452**	**0.967**	0.779	4.371	3.091	**2.186**	**6.557**	3.884
Green. halibut	0.008	0.005	**0.004**	**0.011**	0.009	0.044	0.049	**0.010**	**0.079**	0.042
Small Amer. plaice	1.911	0.473	**1.370**	**2.383**	1.400	15.835	13.385	**6.371**	**25.299**	8.071
Large Amer. plaice	0.244	0.038	**0.212**	**0.277**	0.235	1.497	1.339	**0.549**	**2.444**	1.176
Flounders	0.344	0.126	**0.274**	**0.465**	0.465	3.262	2.405	**1.561**	**4.962**	2.601
Skates	0.016	0.004	**0.014**	**0.020**	0.017	0.175	0.135	**0.080**	**0.270**	0.095
Redfish	0.006	0.004	**0.002**	**0.009**	0.009	0.184	0.220	**0.028**	**0.340**	0.049
Large demersals	0.115	0.021	**0.093**	**0.135**	0.122	0.850	0.666	**0.379**	**1.321**	0.412
Small demersals	0.219	0.288	**0.015**	**0.422**	0.420	2.127	1.771	**0.875**	**3.379**	1.523
Capelin	0.304	0.429	**0.001**	**0.608**	0.549	13.686	18.663	**0.489**	**26.882**	2.674

Table 19. Cont.

	Production (t km^{-2} yr^{-1})					Consumption (t km^{-2} yr^{-1})				
Group	Mean	± SD	Min	Max	Est.	Mean	± SD	Min	Max	Est.
Large pelagics	0.006	0.005	**0.003**	**0.011**	0.009	0.191	0.231	**0.028**	**0.354**	0.044
Pisci. small pel. feeders	1.093	0.496	**0.749**	**1.537**	1.247	17.290	17.475	**4.933**	**29.647**	6.750
Plank. small pel. feeders	3.215	0.641	**2.710**	**3.922**	3.433	86.434	107.081	**10.716**	**162.151**	19.858
Shrimp	1.161	1.640	**0.001**	**2.320**	1.614	7.738	5.472	**3.869**	**11.607**	6.933
Large crustaceans	0.841	0.145	**0.739**	**0.944**	0.921	5.703	3.833	**2.993**	**8.414**	3.986
Echinoderms	33.667	38.755	**0.108**	**70.108**	33.343	243.147	185.156	**112.222**	**374.072**	145.205
Molluscs	22.949	34.282	**0.600**	**82.121**	49.108	165.744	126.214	**76.497**	**254.991**	180.390
Polychaetes	16.680	24.487	**0.206**	**74.564**	30.808	120.468	91.737	**55.601**	**185.336**	119.932
Other benthic invertebrates	9.173	7.631	**0.517**	**15.677**	9.425	66.252	50.451	**30.578**	**101.926**	47.813
Large zooplankton	18.520	19.629	**4.640**	**32.400**	24.570	127.154	114.245	**46.370**	**207.938**	170.006
Small zooplankton	232.943	159.725	**120.000**	**345.886**	321.192	996.401	789.507	**438.135**	**1554.666**	1138.283
Phytoplankton	1763.773	780.945	**982.828**	**2544.718**	1307.722					
Detritus										

[a]: Calculated as $P_X * CV(P_Y)_{mean}$ with $CV(P_Y)_{mean}$ = 71%, the average of all coefficients of variation for observed production.

Table 20. Observed production and consumption used as input parameters for modelling for the 1994–1996 period in the southern Gulf of St. Lawrence. SD: standard deviation, Min: minimum, Max: maximum. Est: value estimates by inverse modelling. Values used in data equations or as upper and lower limit constraints are indicated in boldface. Means and SDs were calculated on the two extreme values.

	Production (t km^{-2} yr^{-1})					Consumption (t km^{-2} yr^{-1})				
Group	Mean	± SD	Min	Max	Est.	Mean	± SD	Min	Max	Est.
Cetaceans	0.0029	0.0025[a]			0.0029	0.322	0.040	**0.293**	**0.350**	0.302
Harp seals	0.027	0.022	**0.011**	**0.043**	0.013	2.678	2.234	**1.098**	**4.257**	1.433
Hooded seals	**0.0004**	0.0002	0.0002	0.0005	0.0004	0.045	0.014	**0.035**	**0.055**	0.044
Grey seals	0.0070	0.0058	**0.0029**	**0.0111**	0.0084	0.659	0.638	**0.207**	**1.110**	1.008
Harbour seals	0.00025	0.00024	**0.00008**	**0.00042**	0.00014	0.025	0.024	**0.008**	**0.042**	0.018
Seabirds	**0.0011**	0.0009[a]			0.0011	0.309	0.280	**0.111**	**0.507**	0.131
Large cod	0.573	0.191	**0.429**	**0.699**	0.429	3.818	2.700	**1.909**	**5.727**	3.512
Small cod	0.157	0.013	**0.127**	**0.189**	0.171	1.047	0.741	**0.524**	**1.571**	1.165
Green. halibut	0.005	0.005	**0.001**	**0.008**	0.008	0.029	0.028	**0.009**	**0.049**	0.035
Small Amer. plaice	1.518	0.343	**1.195**	**1.981**	1.504	13.048	11.295	**5.061**	**21.035**	10.530
Large Amer. plaice	0.087	0.006	**0.080**	**0.095**	0.092	0.577	0.411	**0.286**	**0.867**	0.591
Flounders	0.337	0.105	**0.268**	**0.440**	0.437	3.369	2.421	**1.657**	**5.081**	2.897
Skates	0.008	0.002	**0.007**	**0.010**	0.010	0.086	0.065	**0.040**	**0.132**	0.046
Redfish	0.004	0.004	**0.001**	**0.007**	0.007	0.142	0.174	**0.019**	**0.264**	0.039
Large demersals	0.044	0.051	**0.008**	**0.080**	0.073	0.724	0.716	**0.218**	**1.230**	0.244
Small demersals	0.076	0.067	**0.028**	**0.124**	0.124	1.039	1.039	**0.304**	**1.773**	0.415
Capelin	11.317	17.858	**2.305**	**29.287**	2.942	683.258	935.828	**21.528**	**1344.989**	22.617

Table 20. Cont.

	Production (t km^{-2} yr^{-1})					Consumption (t km^{-2} yr^{-1})				
Group	Mean	± SD	Min	Max	Est.	Mean	± SD	Min	Max	Est.
Large pelagics	0.030	0.020	**0.015**	**0.044**	0.036	1.197	1.495	**0.140**	**2.254**	0.148
Pisci. small pel. feeders	0.399	0.225	**0.275**	**0.533**	0.428	4.516	4.751	**1.157**	**7.876**	2.637
Plank. small pel. feeders	2.946	0.100	**2.789**	**3.121**	3.036	56.829	66.482	**9.819**	**103.839**	19.667
Shrimp	2.434	3.400	**0.030**	**4.838**	2.414	16.227	11.474	**8.113**	**24.340**	15.645
Large crustaceans	0.944	0.197	**0.823**	**1.074**	0.972	6.235	4.529	**3.032**	**9.437**	5.995
Echinoderms	33.667	38.755	**0.108**	**70.108**	39.495	243.147	185.156	**112.222**	**374.072**	174.811
Molluscs	22.949	34.282	**0.600**	**82.121**	44.024	165.744	126.214	**76.497**	**254.991**	185.903
Polychaetes	16.680	24.487	**0.206**	**74.564**	31.119	120.468	91.737	**55.601**	**185.336**	139.087
Other benthic invertebrates	9.173	7.631	**0.517**	**15.677**	8.955	66.252	50.451	**30.578**	**101.926**	55.838
Large zooplankton	26.000	19.799	**12.000**	**40.000**	33.516	153.185	151.059	**46.370**	**260.000**	210.505
Small zooplankton	232.943	159.725	**120.000**	**345.886**	331.510	996.401	789.507	**438.135**	**1554.666**	1218.645
Phytoplankton	1763.773	780.945	**982.828**	**2544.718**	1548.319					
Detritus										

[a]: Calculated as P_X*$CV(P_Y)_{mean}$ with $CV(P_Y)_{mean}$ = 73%, the average of all coefficients of variation for observed production.

DISCUSSION

The CDEENA project focussed on the comparison of different ecosystems (northern and southern Gulf of St. Lawrence, Newfoundland–Labrador Shelf, Scotian Shelf) for different time periods, i.e., the pre-collapse period (1985–1987) and the post-collapse period (1994–1996) in the groundfish stocks. The time periods were determined after the analysis of biomass fluctuations for the key groundfish species of the system (i.e., cod, Greenland halibut, and redfish) in the pre- and the post-collapse periods. These time periods were chosen in order to have no year-to-year change in biomass during the modelled periods. The present data sets were used to construct models of the southern Gulf of St. Lawrence for the two periods.

The validity of any conclusions regarding the ecosystem being studied depends on the input data (and the confidence one might have in them). The strengths and weaknesses of these inputs have to be judged. There are two levels of uncertainties in all mass-balance models. One level is which components (boxes and flows in the mass-balance models) to include in the starting configuration; the other level is the uncertainty of what the starting values should be for the minimum number of components that constrain the parameter estimation step.

Uncertainty in the input data

Ecosystem modelling requires the collection of a considerable amount of information. The modelling results described here were influenced by several areas of uncertainty for different groups at all trophic levels. The quality of input data was variable. Landing estimates are considered quite reliable. However, in the northern Gulf of St. Lawrence, there is indirect but reliable evidence for non-negligible misreporting (non-reported landings and discards at sea) (Fréchet 1991; Hurtubise et al. 1992; Palmer and Sinclair 1997). We might expect similar unreported catches in the southern Gulf. Uncertainty also occurs for the catch estimates of small cod and small American plaice, which was assumed to be negligible. Indeed, it is known that discarding of small American plaice was substantial during some periods such as the 1980s (Tallman 1991).

Biomass estimates for demersal fish were based on catches in a bottom-trawl survey conducted in the southern Gulf each September. These survey estimates were converted to estimates of total biomass using the catchability coefficients reported by Harley and Myers (2001). These coefficients are generic and also contribute to the model uncertainty. Also, biomass estimates for several other model compartments (seals, herring, mackerel, large crustaceans) were based on data from other surveys or population models. In other cases, biomass was based on densities reported for other ecosystems (e.g., other benthic invertebrates) or was estimated by the initial models to meet predator demands (e.g., small demersals, capelin, shrimp).

Very little is known about the fish and invertebrate production and consumption in the Gulf of St. Lawrence. For fish, the majority of the production estimates were obtained assuming that production or total mortality is equivalent to biomass multiplied by natural mortality, plus the catch in the absence of information on total mortality under the steady-state assumption. Unfortunately, we had few measures of natural mortality. In many cases, we assumed that natural mortality was equal to a fixed value in order to get a preliminary production estimate that was then allowed to vary over a wide range. For large cod only, production was based on mortality

rates estimated using a modified catch curve analysis of the survey data (Sinclair 2001). It was also necessary to use empirical data from other areas and/or time frames (e.g., capelin, shrimp), or less specific information (e.g., pelagic feeders, benthic invertebrates) for production and consumption estimates.

Diet composition was based on samples from the southern Gulf where possible. However, these data do not exist for some species (e.g., Greenland halibut, redfish, capelin, and shrimp). For these species, diet data were taken from the same area but for another time period or from the literature for other areas and/or time periods. Further uncertainties with diet data resulted from assuming that the diet for a key species is representative of the functional group to which it belonged, or attributing the proportion of "unidentified" in stomach content analysis in proportion to the different identified groups in the stomachs. Based on the different sources of the data (local and literature), we estimated the lower and upper limits of each diet proportion used as input in inverse modelling. Means and standard deviations were calculated either directly from the lower and upper limits when there was no information on number of stomachs or from the different diet proportions, which were weighted by the number of stomachs when stomach content analyses were given.

The uncertainties remaining in the understanding of the ecosystem may come from incorrect values used because no data exist, confidence limits that are too large, or inaccurate aggregation of species within one functional group, as well as from unsuspected processes occurring in the ecosystem. Overall, even though the model is not a perfect representation of reality, it is probably as good as we can get with the information available.

Strengths and weaknesses of the modelling efforts

The synthesis of existing ecosystem information is designed to enable a whole-system view using parameters that are basic to understanding populations and the ecosystem (Okey and Pauly 1999). Compared to single-species models, multispecies mass-balance models improve our understanding of the dynamics of fish populations through a more realistic treatment of uncertainty and variability in population parameters (e.g., natural mortality) or by identifying additional non-target species and ecological linkages among species, which could be altered through fishing (Hollowed et al. 2000; Whipple et al. 2000). Among the multispecies models, inverse models are static-flow models that provide a "snapshot" of the system at one moment in time and use mass-balance principles and an objective least-squares criterion to estimate flows of organic matter or energy among components of an ecosystem. The use of upper and lower limits to constrain the majority of input values (production, consumption, and diet composition) and the choice of row and column weights make inverse modelling a flexible tool to quantify mass-balanced flow diagrams and trophic transfer efficiencies that are internally consistent.

However, due to the fact that our empirical databases and scientific understanding of ecological processes will always be incomplete (i.e., underdetermined system: the number of flows to be solved exceeds the number of independent mass balance relations), flow network solutions are not unique. Different approaches (comparisons of different flow networks, random perturbations, sensitivity tests) have to be used to allow for an explicit implementation and assessment of this uncertainty (or the solution's robustness) to variations in the data (Whipple et al. 2000). Indeed, mass-balance models estimated a very large number of parameters and it is

possible that the relatively limited data available were insufficient to constrain these parameters. Also, where one modelling approach compromises or simplifies portions of the system, another may provide a realistic and precise representation of the same parts of the system. In this study, by randomly perturbing data inputs, we constructed a set of balanced solutions and we used the mean of these 31 random perturbations. The estimated flows fall inside our a priori constraints (once the data are perturbed) and therefore are a reasonable "middle ground" description.

The model provides an overall view of the ecosystem, identifies general robust patterns, and shows where the uncertainties in the food web occur, which could be examined in future studies. Some progress is still needed in understanding and refining the structure of ecosystems in the Gulf of St. Lawrence as well as in other areas of the world.

CONCLUSION

This work is the result of a huge effort to assemble data on the biological characteristics of species occurring in the southern Gulf of St. Lawrence. Even though most of the data are good estimates for the 4T ecosystem during the 1985–1987 and 1994–1996 periods, some other input values are rough estimates only, meaning that these values are assembled from different literature sources and not from independently measured parameters. Some errors in parameter estimates could significantly alter the system's biomass budget, especially for the most important species of the ecosystem, or produce a totally different balanced solution. Although the top predators appear to be reasonably represented, there is an evident lack of data on particular key species such as capelin, shrimp, benthic invertebrates, and planktonic species (especially euphausiids, mysids, and jellyfish). This illustrates the need for further work to improve the input parameters in order to enhance the quality of future modelling efforts. In conclusion, this model enabled us to bring together wide-ranging data concerning the southern Gulf of St. Lawrence ecosystem. By doing so, it allowed us to focus attention on uncertainties in our knowledge of the ecosystem's structure and to identify where research efforts should be directed if we are to gain a better understanding of this ecosystem.

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See the CDEENA web site at http://www.osl.gc.ca/cdeena/en/accueil.shtml.

REFERENCES

Ajiad, A. M., and T. Pushaeva. 1991. The daily feeding dynamics in various length groups of the Barents Sea capelin during the feeding period. ICES Council Meeting Papers 1991/H16, 21 p.

Allen, K. R. 1971. Relation between production and biomass. Journal of Fisheries Research Board of Canada **28**: 1573-1581.

Atkinson, D. B., and B. R. Melteff. 1987. The redfish resources off Canada's east coast. *In* Lowell Wakefield Fisheries Symposium: Proceedings of the International Rockfish Symposium, Anchorage, Alaska, USA, October 20-22 1986, pp. 15-33.

Beck, G. G., M. O. Hammill and T. G. Smith. 1993. Seasonal variation in the diet of harp seals (*Phoca groenlandica*) from the Gulf of St. Lawrence and western Hudson Strait. Canadian Journal of Fisheries and Aquatic Sciences **50**: 1363-1371.

Benoit, D., and W. D. Bowen. 1990. Summer diet of grey seals (*Halichoerus grypus*) at Anticosti Island, Gulf of St. Lawrence, Canada. *In* Population biology of the sealworm (*Pseudoterranova decipiens*) in relation to its intermediate and seal hosts. *Edited by* W. D. Bowen. Canadian Bulletin of Fisheries and Aquatic Sciences **222**, pp. 227-242.

Berkes, F. 1977. Production of the euphausiid crustacean *Thysanoëa rashii* in the Gulf of St. Lawrence. Journal of the Fisheries Research Board of Canada **34**: 443-446.

Bigelow, H. B., and W. C. Schroeder. 1953. Fishes of the Gulf of Maine. Fishery Bulletin, U.S. Fish & Wildlife Service 74(53).

Borkowski, T. V. 1974. Growth, mortality and productivity of south Floridian Littorinidae (*Gastropoda: Prosobranchia*). Bulletin of Marine Science **24**: 409-438.

Boulva, J., and I. A. McLaren. 1979. Biology of the harbor seal, *Phoca vitulina*, in eastern Canada. Bulletin of the Fisheries Research Board of Canada **200**, 32 pp.

Bowen, W. D., and G. D. Harrison. 1996. Comparison of harbour seal diets in two inshore habitats of Atlantic Canada. Canadian Journal of Zoology **74**: 125-135.

Bowering, W. R. 1983. Age, growth and sexual maturity of Greenland halibut, *Reinhardtius hippoglossoides* (Walbaum), in the Canadian northwest Atlantic. Fishery Bulletin **81**: 599-611.

Brêthes, J.-C., G. Desrosiers and F. Coulmobe. 1984. Aspects de l'alimentation et du comportement alimentaire du crabe-des-neiges, *Chionoectes opilio* (O. Fabr.) dans le sud-ouest du golfe de St-Laurent (Decapoda, Brachyura). Crustaceana **47**: 235-244.

Brown, R. G. B. 1986. Revised atlas of eastern Canadian seabirds. I. Shipboard surveys. Ottawa, Canadian Wildlife Service, 111 pp.

Buchanan, J. B., and R. M. Warwick. 1974. An estimate of benthic macrofaunal production in the offshore mud of the Northumberland coast. Journal of the Marine Biological Association of the United Kingdom **54**: 197-222.

Bundy, A., G. R. Lilly and P. A. Shelton. 2000. A Mass Balance Model of the Newfoundland-Labrador Shelf. Canadian Technical Report of Fisheries and Aquatic Sciences No. 2310.

Burton, J. 1980. L'alimentation estivale du fou de Bassan (*Sula bassana L.*) au Rocher aux Oiseaux, Îles-de-la-Madelaine, Québec. Naturaliste canadien **107**: 289-291.

Cairns, D. K. 1981. Breeding, feeding and chick growth of the black guillemot (*Cepphus grylle*) in southern Quebec. Canadian Field-Naturalist **95**: 312-318.

Cairns, D. K., W. A. Montevecchi, V. L. Birt-Friesen and S. A. Macko. 1990. Energy expenditures, activity budgets, and prey harvest of breeding common murres. Studies in Avian Biology **14**: 84-92.

Cairns, D. K., G. Chapdelaine and W. A. Montevecchi. 1991. Prey exploitation by seabirds in the Gulf of St. Lawrence. *In* The Gulf of St. Lawrence: small ocean or big estuary? *Edited by* J.-C. Therriault. Canadian Special Publication of Fisheries and Aquatic Sciences **113**, pp. 227-291.

Caswell, H., S. Brault, A. J. Read and T. D. Smith. 1998. Harbor porpoise and fisheries: An uncertainty analysis of incidental mortality. Ecological Applications **8**: 1226-1238.

Cederwall, H. 1977. Annual macrofauna production of a soft bottom in the northern Baltic proper. *In* Biology of benthic organisms. *Edited by* B. F. Keegan, P. O. Ceidigh and P. J. S. Boaden. European Symposium on Marine Biology, Galway (Eire), 5 Oct 1976, Oxford (UK), Pergamon Press, pp. 155-164.

Chabot, D., and G. B. Stenson. 2002. Growth and seasonal fluctuations in size and condition of male Northwest Atlantic harp seals *Phoca groenlandica*: An analysis using sequential growth curves. Marine Ecology Progress Series **227**: 25-42.

Chapdelaine, G., P. Brousseau, R. Anderson and R. Marsan. 1985. Breeding ecology of common and Arctic terns in the Mingan Archipelago, Québec. Colonial Waterbirds **8**: 166-177.

Chouinard, G. A., A. F. Sinclair, L. Currie, G. Poirier and D. P. Swain. 1999. Assessment of cod in the southern Gulf of St. Lawrence, March 1999. Canadian Stock Assessment Secretariat Research Document 1999/023.

Chouinard, G. A., D. P. Swain, L. Currie, G. A. Poirier, A. Rondeau, H. Benoit T. Hurlbut, and D. Daigle. 2003. Assessment of the southern Gulf of St. Lawrence cod stock, February 2003. Canadian Stock Assessment Secretariat Research Document 2003/015.

Christensen, V., and D. Pauly. 1992. ECOPATH II - A system for balancing steady-state ecosystem models and calculating network characteristics. Ecological Modelling **61**: 169-185.

Christensen, V., and D. Pauly (*Editors*). 1993. Trophic models of aquatic ecosystems. ICLARM Conference Proceedings 26, 390 pp.

Christensen, V., and D. Pauly. 1998. Changes in models of aquatic ecosystems approaching carrying capacity. Ecological Applications **8** (Suppl.): S104-S109.

Christensen, V., C. J. Walters and D. Pauly. 2000. Ecopath with Ecosim: a User's Guide. October 2000 Edition, Fisheries Centre, The University of British Columbia, Vancouver, Canada and ICLARM, Penang, Malaysia, 130 pp.

Chumakov, A. K., and S. G. Podrazhanskaya. 1986. Feeding of Greenland halibut (*Reinhardtius hippoglossoides*) in the northwest Atlantic. NAFO Scientific Council Studies **10**: 47-52.

Cohen, E., and M. Grosselin. 1981. Food consumption in five species of fish on Georges Bank. ICES Council Meeting Papers 1981/G 68, 21 pp.

Collie, J. S. 1985. Life history and production of three amphipod species on Georges Bank. Marine Ecology Progress Series **22**: 229-238.

Collie, J. S. 1987. Food consumption by yellowtail flounder in relation to production of its benthic prey. Marine Ecology Progress Series **36**: 205-213.

Curtis, M. A. 1977. Life cycles and population dynamics of marine benthic polychaetes from the Disko Bay area of West Greenland. Ophelia **16**: 9-58.

de Lafontaine, Y., S. Demers and J. Runge. 1991. Pelagic food web interactions and productivity in the Gulf of St. Lawrence: A perspective. *In* The Gulf of St. Lawrence: small ocean or big estuary? *Edited by* J. C. Therriault. Canadian Special Publication of Fisheries and Aquatic Sciences **113**, pp. 99-123.

Desrosiers, G., C. Savenkoff, M. Olivier, G. Stora, K. Juniper, A. Caron, J.-P. Gagné, L. Legendre, S. Mulsow, J. Grant, S. Roy, A. Grehan, P. Scaps, N. Silverberg, B. Klein, J.-E. Tremblay and J.-C. Therriault. 2000. Trophic structure of macrobenthos in the Gulf of St. Lawrence and on the Scotian Shelf. Deep-Sea Research II **47**: 663-697.

DFO. 2002a. Cod in the southern Gulf of St. Lawrence. DFO Science, Stock Status Report A3-01.

DFO. 2002b. Gulf of St. Lawrence (4RST) Greenland halibut in 2001. DFO Science, Stock Status Report A4-03.

DFO. 2002c. Maquereau bleu du nord-ouest de l'Atlantique. MPO Rapport sur l'état des stocks pélagiques B4-O4.

Dolgov, A. V. 1997. Distribution, abundance, biomass and feeding of thorny skate, *Raja radiata*, in the Barents Sea. ICES Council Meeting Papers 1997/G:04, 21 pp.

Dolgov, A. V., and K. V. Revetnyak. 1990. Estimation of rations and food consumption of deep-water redfish (*Sebastes mentella*) from the Norwegian-Barents Sea stock. ICES Council Meeting Papers 1990/G:11, 15 pp.

Elliott, J. M., and L. Persson. 1978. The estimation of daily rates of food consumption for fish. Journal of Animal Ecology **47**: 977-991.

Fauchald, K., and P. A. Jumars. 1979. The diet of worms: a study of polychaete feeding guilds. Oceanography and Marine Biological Annual Review **17**: 19-38.

Fetter, M., and A. Davidjuka. 1996. Herring daily feeding activity in the Eastern Baltic. ICES Council Meeting Papers 1996/J 26, 10 pp.

Fontaine, P. M., C. Barrette, M. O. Hammill and M. C. Kingsley. 1994a. Incidental catches of harbour porpoises (*Phocoena phocoena*) in the Gulf of St. Lawrence and the St. Lawrence River Estuary, Québec, Canada. Report of the International Whaling Commission Special Issue 15: 159-163.

Fontaine, P. M., M. O. Hammill, C. Barrette and M. C. Kingsley. 1994b. Summer diet of the harbour porpoise (*Phocoena phocoena*) in the estuary and the northern Gulf of St. Lawrence. Canadian Journal of Fisheries and Aquatic Sciences **51**: 172-178.

Fréchet, A. 1991. A declining cod stock in the Gulf of St. Lawrence: how can we learn from the past? NAFO Scientific Council Studies **16**: 95-102.

Fréchette, J., and S. S. M. Labonté. 1981. Biomass estimate, year-class abundance and mortality rates of *Pandalus borealis* in the northwest Gulf of St. Lawrence. *In* Proceedings of the International Pandalid Shrimp Symposium. *Edited by* T. Frady. Kodiac, Alaska, Sea Grant Report 81-3, pp. 307-330.

Froese, R., and D. Pauly. 1995. FishBase, a biological database on fish - concepts, design and data sources. ICLARM, Manilla, Philippines, 146 pp.

Froese, R., and D. Pauly (Eds.). 2002. FishBase. World Wide Web electronic publication. [On line 25 September 2002] http://www.fishbase.org.

Grégoire, F., and M. Castonguay. 1989. L'alimentation du maquereau bleu (*Scomber scombrus*) dans le golfe du St-Laurent et sur le plateau néo-écossais, avec une application du test de Mantel. Rapport technique canadien des sciences halieutiques et aquatiques No. 1673.

Hammill, M. O., and G. B. Stenson. 2000. Estimated prey consumption by harp seals (*Phoca groenlandica*), hooded seals (*Cystophora cristata*), grey seals (*Halichoerus grypus*) and harbour seals (*Phoca vitulina*) in Atlantic Canada. Journal of Northwest Atlantic Fishery Science **26**: 1-23.

Hammill, M. O., C. Lydersen, K. M. Kovacs and B. Sjare. 1997. Estimated fish consumption by hooded seals (*Cystophora cristata*) in the Gulf of St. Lawrence. Journal of Northwest Atlantic Fishery Science **22**: 249-257.

Hammill, M. O., G. B. Stenson, R. A. Myers and W. T. Stobo. 1998. Pup production and population trends of the grey seal (*Halichoerus grypus*) in the Gulf of St. Lawrence. Canadian Journal of Fisheries and Aquatic Sciences **55**: 423-430.

Hanson, J. M., and G. A. Chouinard. 2002. Diet of Atlantic cod in the southern Gulf of St Lawrence as an index of ecosystem change, 1959-2000. Journal of Fish Biology **60**: 902-922.

Hanson, J. M., and M. Lanteigne. 1999. Results of an experimental shrimp fishery in Chaleur Bay, southern Gulf of St. Lawrence. North American Journal of Fisheries Management **19**: 713-723.

Hanson, J. M., and M. Lanteigne. 2000. Evaluation of Atlantic cod predation on American lobster in the southern Gulf of St. Lawrence, with comments on other potential fish predators. Transactions of the American Fisheries Society **129**: 13-29.

Harley, S. J., and R. A. Myers. 2001. Hierarchical Bayesian models of length-specific catchability of research trawl surveys. Canadian Journal of Fisheries and Aquatic Sciences **58**: 1569-1584.

Harris, R., P. Wiebe, J. Lenz, H. R. Skjoldal and M. Huntley. 2000. ICES Zooplankton Methodology Manual. Academic Press, San Diego, 684 pp.

Haycock, K. A., and W. Threlfall. 1975. The breeding biology of the herring gull in Newfoundland. Auk **92**: 678-697.

Healey, B. P., and G. B. Stenson. 2000. Estimating pup production and population size of the northwest Atlantic harp seal (*Phoca groenlandica*). DFO Canadian Stock Assessment Secretariat Research Document 2000/081.

Hébert M., E. Wade, T. Surette and M. Moriyasu. 2002. The 2001 assessment of snow crab, *Chionoecetes opilio*, stock in the southern Gulf of St. Lawrence (Areas 12, E and F). DFO Canadian Stock Assessment Secretariat research document 2002/013.

Heise, K. 1997. Life history and population parameters of Pacific white-sided dolphins (*Lagenorhynchus obliquidens*). Annual Report International Whaling Commission **47**: 817-825.

Hollowed, A. B., N. Bax, R. Beamish, J. Collie, M. Fogarty, P. Livingston, J. Pope and J. C. Rice. 2000. Are multispecies models an improvement on single-species models for measuring fishing impacts on marine ecosystems? ICES Journal of Marine Sciences **57**: 707-719.

Hop, H., W. M. Tonn and H. E. Welch. 1997. Bioenergetics of Arctic cod (*Boreogadus saida*) at low temperatures. Canadian Journal of Fisheries and Aquatic Sciences **54**: 1772-1784.

Horwood, J. 1990. Biology and exploitation of the minke whale. CRC Press, Boca Raton, FL (USA), 238 pp.

Hurtubise, S., A. Fréchet and L. Savard. 1992. Les captures accessoires sur les crevettiers et les sebastiers du golfe du Saint-Laurent. NAFO Scientific Council Research Document 92/60, 14 pp.

Hutcheson, M., P. Stuwart and J. Spry. 1981. The biology of benthic communities on the Grand Banks of Newfoundland (including the Hibernia area). *In* Grand Banks Oceanographic Studies 3. *Edited by* MacLaren Plansearch, prepared for Mobil Oil, 99 pp.

Katona, S. K., S. A. Testaverde and B. Barr. 1978. Observations on a white-sided dolphin, *Lagenorhynchus acutus*, probably killed in gill nets in the Gulf of Maine. Fishery Bulletin **76**: 475-476.

Kenney, R. D., G. P. Scott, T. J. Thompson and H. E. Winn. 1997. Estimates of prey consumption and trophic impacts of cetaceans in the USA northeast continental shelf ecosystem. Journal of Northwest Atlantic Fishery Science **22**: 155-171.

Kingsley, M. C. S., and R. R. Reeves. 1998. Aerial surveys of cetaceans in the Gulf of St. Lawrence in 1995 and 1996. Canadian Journal of Zoology **76**: 1529-1550.

Klein, G., E. Rachor and S. A. Gerlach. 1975. Dynamics and productivity of two populations of the benthic tube-dwelling amphipod *Ampelisca brevicornis* (Costa) in Helgoland Bight. Ophelia **14**: 1-2.

Lack, D. 1967. Interrelationships in breeding adaptations as shown by marine birds. Proceedings of the XIV International Ornithology Congress, pp. 3-42.

Langton, R. W., and R. E. Bowman. 1980. Food of fifteen northwest Atlantic gadiform fishes. NOAA Technical Report NMFS SSRF-740, 23 pp.

Lawson, J. W., G. B. Stenson and D. G. McKinnon. 1993. Diet of harp seals (*Phoca groenlandica*) in 2J3KL during 1991–1993. NAFO Scientific Council Research Document 93/36, 15 pp.

Lawson, J. W., G. B. Stenson and D. G. McKinnon. 1995. Diet of harp seals (*Phoca groenlandica*) in nearshore waters of the northwest Atlantic during 1990–1993. Canadian Journal of Zoology **73**: 1805-1818.

Leblanc, M.-J. 2003. Variations saisonnières en taille et en condition du phoque à capuchon (*Cystophora cristata*) dans le nord-ouest de l'Atlantique. M.Sc. Thesis. Université du Québec à Rimouski.

Leblanc, C. H., G. A. Chouinard and G. A. Poirier. 2001. Assessment of the NAFO 4T southern Gulf of St. Lawrence herring stocks in 2000. DFO Canadian Stock Assessment Secretariat Research Document 2001/045.

Lesage, V., M. O. Hammill and K. M. Kovacs. 1995. Harbour seal (*Phoca vitulina*) and grey seal (*Halichoerus grypus*) abundance in the St. Lawrence Estuary. Canadian Manuscript Report of Fisheries and Aquatic Sciences No. 2307.

Lien, J. 1985. Wet and fat: Whales and seals of Newfoundland and Labrador. Breakwater Books, St. John's, Newfoundland, 136 pp.

Lilly, G. R. 1991. Interannual variability in predation by cod (*Gadus morhua*) on capelin (*Mallotus villosus*) and other prey off southern Labrador and northeastern Newfoundland. ICES Marine Science Symposia **193**: 133-146.

Lilly, G. R., H. Hop, D. E. Stansbury and C. A. Bishop. 1994. Distribution and abundance of polar cod (*Boreogadus saida*) off southern Labrador and eastern Newfoundland. ICES Council Meeting Papers 1994/O 6, 21 pp.

Lindley, J. A. 1980. Population dynamics and production of euphausiids. 2. *Thysanoessa inermis* and *T. raschi* in the North Sea and American coastal waters. Marine Biology **59**: 225-233.

Lindley, J. A. 1982. Population dynamics and production of euphausiids. 3. *Meganyctiphanes norvegica* and *Nyctiphanes couchi* in the North Atlantic Ocean and the North Sea. Marine Biology **66**: 37-46.

MacDonald, J. S., and K. G. Waiwood. 1987. Feeding chronology and daily ration calculations for winter flounder (*Pseudopleuronectes americanus*), American plaice (*Hippoglossoides platessoides*), and ocean pout (*Macrozoarces americanus*) in Passamaquody Bay, New Brunswick. Canadian Journal of Zoology **65**: 499-503.

Mansfield, A. W., and B. Beck. 1977. The grey seal in eastern Canada. Fisheries and Marine Service Technical Report 704, 81 pp.

Marsh, H., and D. F. Sinclair. 1989. Correcting for visibility bias in strip transect aerial surveys of aquatic fauna. Journal of Wildlife Management **53**: 1017-1024.

Martin, A. R. 1990. Whales and dolphins. Salamander Press, London and New York, 192 pp.

Mauchline, J. 1980. The biology of euphausiids. Advances in Marine Biology **18**: 373-623.

Mauchline, J. 1985. Growth and production of Euphausiacea (Crustacea) in the Rockall Trough. Marine Biology **90**: 19-26.

Maunder, J. E., and W. Threlfall. 1972. The breeding biology of the black-legged kittiwake in Newfoundland. Auk **89**: 789-816.

McEachran, J. D., D. F. Boesch and J. A. Musick. 1976. Food division within two sympatric species-pairs of skates (*Pisces: Rajidae*). Marine Biology **35**: 301-317.

McKone, W. D., and E. LeGrow. 1983. Thorny and smooth skates. DFO Underwater world series UW/21.

Mehl, S., and T. Westgard. 1983. The diet and consumption of mackerel in the North Sea (a preliminary report). ICES Council Meeting Papers 1983/H 34, 30 pp.

Montevecchi, W. A., and L. M. Tuck. 1987. Newfoundland birds: exploitation, study, conservation. Cambridge, Massachusetts, USA, Nuttal Ornithological Club, 272 pp.

Moores, J. A., G. H. Winters and L. S. Parsons. 1975. Migrations and biological characteristics of Atlantic mackerel (*Scomber scombrus*) occurring in Newfoundland waters. Journal of the Fisheries Research Board of Canada **32**: 1347-1357.

Morin, R., G. A. Chouinard, I. Forest-Gallant and G. Poirier. 1998. Assessment of 4T American plaice in 1996 and 1997. DFO Canadian Stock Assessment Secretariat Research Document 98/06.

Morissette, L., S.-P. Despatie, C. Savenkoff, M. O. Hammill, H. Bourdages and D. Chabot. 2003. Data gathering and input parameters to construct ecosystem models for the northern Gulf of St. Lawrence (mid-1980s). Canadian Technical Report of Fisheries and Aquatic Sciences No. 2497.

Murie, D. J., and D. M. Lavigne. 1991. Food consumption of wintering harp seals, *Phoca groenlandica*, in the St. Lawrence estuary, Canada. Canadian Journal of Zoology **69**: 1289-1296.

Murie, D. J., and D. M. Lavigne. 1992. Growth and feeding habits of grey seals (*Halichoerus grypus*) in the northwestern Gulf of St. Lawrence, Canada. Canadian Journal of Zoology **70**: 1604-1613.

NAFO (*Editors*). 1999. NAFO Statistical information. World Wide Web electronic publication. [On line September 1999] http://www.nafo.ca.

Nesis, K. I. 1965. Bioeconoses and biomass of benthos of the Newfoundland-Labrador region. Fisheries Research Board of Canada Translation Series **1357**, 75 pp.

Ni, I.-H. 1982. Meristic variation in beaked redfish, *Sebastes mentella* and *S. fasciatus*, in the Northwest Atlantic. Canadian Journal of Fisheries and Aquatic Sciences **39**: 1664-1685.

Nichols, F. H. 1975. Dynamics and energetics of three deposit-feeding benthic invertebrate populations in Puget Sound, Washington. Ecological Monographs **45**: 57-82.

Ohman, M. D., and J. A. Runge. 1994. Sustained fecundity when phytoplankton resources are in short supply: omnivory by *Calanus finmarchicus* in the Gulf of St. Lawrence. Limnology and Oceanography **39**: 21-36.

Ohsumi, S. 1979. Interspecies relationships among some biological parameters in cetaceans and estimation of the natural mortality coefficient of the Southern Hemisphere minke whale. Report of the International Whaling Commission 29: 397-406.

Okey, T. A., and D. Pauly, 1999. A trophic mass-balance model of Alaska's Prince William Sound ecosystem, for the post-spill period 1994–1996. Fisheries Centre Research Report 7, 155 pp.

Palmer, C., and P. Sinclair. 1997. When the fish are gone: ecological disaster and fishers in northwest Newfoundland. Fernwood Publishing, Halifax.

Panasenko, L. D. 1981. Diurnal rhythms and rations of capelin feeding in the Barents Sea. ICES Council Meeting Papers 1981/H 26.

Pauly, D. 1989. Food consumption by tropical and temperate fish populations: some generalisations. Journal of Fish Biology **35** (Supplement A): 11-20.

Pauly, D., M. L. Soriano-Bartz and M. L. D. Palomares. 1993. Improved construction, parametrization and interpretation of steady-state ecosystem models. *In* Trophic Models of Aquatic Ecosystems. *Edited by* V. Christensen and D. Pauly, Manila (Philippines), ICLARM Conference Proceedings 26, pp. 1-13.

Pedersen, S. A., and F. Riget. 1992a. Feeding habits of Greenland halibut, *Reinhardtius hippoglossoides*, in West Greenland waters with special emphasis on predation on shrimp and juvenile redfish. ICES Council Meeting Papers 1992/G:25, 22 pp.

Pedersen, S. A., and F. Riget. 1992b. Feeding habits of redfish, *Sebastes* sp., in West Greenland waters with special emphasis on predation on shrimp. ICES Council Meeting Papers 1992/G 24, 15 pp.

Peer, D. L. 1970. Relation between biomass, productivity, and loss to predators in a population of a marine benthic polychaete, *Pectinaria hyperborea*. Journal of the Fisheries Research Board of Canada **27**: 2143-2153.

Pierroti, R. 1983. Gull-puffin interactions on Great Island, Newfoundland. Biological Conservation **26**: 1-14.

Pitt, T. K. 1973. Food of American plaice (*Hippoglossoides platessoides*) from the Grand Bank, Newfoundland. Journal of the Fisheries Research Board of Canada **30**: 1261-1273.

Pitt, T. K. 1982. Recalculation of natural mortality of American plaice from the Grand Bank. NAFO Scientific Council Research Document 82/VI/48, 6 pp.

Proust, F. 1996. Composition du régime alimentaire du phoque gris (*Halichoerus grypus*) dans le Golfe du Saint-Laurent, Québec, Canada. M.Sc. Thesis. Université du Québec à Rimouski, 72 pp.

Rice, J., and D. Rivard. 2003. Proceedings of the zonal assessment meeting – Atlantic cod. Canadian Stock Assessment Secretariat Proceeding Series 2003/021.

Ricker, W. E. 1980. Calcul et interprétation des statistiques biologiques des populations de poissons. Bulletin of the Fisheries Research Board of Canada **191F**, 409 pp.

Rivkin, R. B., L. Legendre, D. Deibel, J.-E. Tremblay, B. Klein, K. Crocker, S. Roy, N. Silverberg, C. Lovejoy, F. Mesplé, N. Romero, M. R. Anderson, P. Matthews, C. Savenkoff and R. G. Ingram. 1996. Vertical flux of biogenic carbon in the ocean: Is there food web control? Science **272**: 1163-1166.

Ross, S. 1993. Food and feeding of the hooded seal in Newfoundland. M.Sc. thesis. Memorial University of Newfoundland, St. John's, Newfoundland.

Roy, S., N. Silverberg, N. Romero, D. Deibel, B. Klein, C. Savenkoff, A. F. Vézina, J.-E. Tremblay, L. Legendre and R. B. Rivkin. 2000. Importance of mesozooplankton feeding for the downward flux of biogenic carbon in the Gulf of St. Lawrence (Canada). Deep-Sea Research II **47**: 519-544.

Rubec, P. J., J. M. McGlade, B. L. Trottier and A. Ferron. 1991. Evaluation of methods for separation of Gulf of St. Lawrence beaked redfish, *Sebastes fasciatus* and *S. mentella*: malate dehydrogenase mobility pattern compared with extrinsic gasbladder muscle passages and anal fin ray counts. Canadian Journal of Fisheries and Aquatic Sciences **48**: 640-660.

Rudstam, L. G., S. Hansson, S. Johansson and U. Larsson. 1992. Dynamics of planktivory in a coastal area of the northern Baltic Sea. Marine Ecology Progress Series **80**: 159-173.

Runge, J. A., M. Castonguay, Y. de Lafontaine, M. Ringuette and J. L. Beaulieu. 1999. Covariation in climate, zooplankton biomass and mackerel recruitment in the southern Gulf of St Lawrence. Fisheries Oceanography **8**: 139-149.

Sameoto, D. D. 1976. Respiration rates, energy budgets, and molting frequencies of three species of euphausiids found in the Gulf of St. Lawrence. Journal of the Fisheries Research Board of Canada **33**: 2568-2576.

Sanders, H. L. 1956. The biology of marine bottom communities. Oceanography of Long Island Sound. X. *In* Oceanography of Long Island Sound, 1952-1954. *Edited by* G. A. Riley, S. A. M. Conover, G. B. Deevey, R. J. Conover, S. B. Wheatland, E. Harriss and H. L. Sanders. Bulletin of the Bingham Oceanography Collection. New Haven, Conn., 15, pp. 345-414.

Savenkoff, C., A. F. Vézina, S. Roy, B. Klein, C. Lovejoy, J.-C. Therriault, L. Legendre, R. Rivkin, C. Bérubé, J.-E. Tremblay and N. Silverberg. 2000. Export of biogenic carbon and structure and dynamics of the pelagic food web in the Gulf of St. Lawrence Part 1. Seasonal variations. Deep-Sea Research II **47**: 585-607.

Savenkoff, C., A. F. Vézina and A. Bundy. 2001. Inverse analysis of the structure and dynamics of the whole Newfoundland–Labrador Shelf ecosystem. Canadian Technical Report of Fisheries and Aquatic Sciences No. 2354.

Savenkoff, C., H. Bourdages, M. Castonguay, L. Morissette, D. Chabot and M. O. Hammill. 2004. Input data and parameter estimates for ecosystem models of the northern Gulf of St. Lawrence (mid-1990s). Canadian Technical Report of Fisheries and Aquatic Sciences (in press).

Scott, W. B., and M. G. Scott. 1988. Atlantic fishes of Canada. Canadian Bulletin of Fisheries and Aquatic Sciences **219**, 731 pp.

Sergeant, D. E. 1991. Harp seals, man and ice. Canadian Special Publication of Fisheries and Aquatic Sciences **114**, 163 pp.

Sergeant, D. E., D. J. St. Aubin and J. R. Geraci. 1980. Life history and northwest Atlantic status of the Atlantic white-sided dolphin, *Lagenorhynchus acutus*. Cetology **37**: 1-12.

Sheader, M. 1977. Production and population dynamics of *Ampelisca tenuicornis* (Amphipoda) with notes on the biology of its parasite *Sphaeronella longipes* (Copepoda). Journal of the Marine Biological Association of the United Kingdom **57**: 955-968.

Silverberg, N., B. Sundby, A. Mucci, S. Zhong, T. Arakaki, P. Hall, A. Landen and A. Tengberg. 2000. Remineralization of organic carbon in eastern Canadian continental margin sediments. Deep-Sea Research II **47**: 699-731.

Simon, J. E., and K. T. Frank. 1996. An assessment of the skate fishery in Division 4VsW. DFO Atlantic Fisheries Research Document 95/71.

Simon, J., L. E. Harris and T. L. Johnson. 2003. Distribution and abundance of winter skate, *Leucoraja ocellata*, in the Canadian Atlantic. DFO Canadian Stock Assessment Secretariat Research Document 2003/028.

Sinclair, A. F. 2001. Natural mortality of cod (*Gadus morhua*) in the southern Gulf of St. Lawrence. ICES Journal of Marine Sciences **58**: 1-10.

Sinclair, A. F., and S. A. Murawski. 1997. Why have groundfish stocks declined? *In* Northwest Atlantic groundfish: perspectives on a fishery collapse. *Edited by* J. Boreman, B.S. Nakashima, J.A. Wilson and R.L. Kendall. American Fisheries Society, Bethesda, MD, pp. 71-93.

Sinclair, A. F., D. P. Swain and J. M. Hanson. 2002. Disentangling the effects of size-selective mortality, density, and temperature on length-at-age. Canadian Journal of Fisheries and Aquatic Sciences **59:** 372-382.

Sjare, B., G. B. Stenson and E. A. Perry. 1996. Summary of the catch and catch-at-age data for harp seals in the northwest Atlantic, 1946-94. NAFO Scientific Council Studies **26**: 33-39.

Smayda, T. J. 1993. Experimental manipulations of phytoplankton + zooplankton + ctenophore communities and foodweb roles of the ctenophore, *Mnemiopsis leidyi*. ICES Council Meeting Papers 1993/L 68, 31 pp.

Squires, H. J. 1990. Decapod crustacea of the Atlantic coast of Canada. Canadian Bulletin of Fisheries and Aquatic Sciences **221**, 532 pp.

Steimle, F. W. J. 1985. Biomass and estimated productivity of the benthic macrofauna in the New York Bight: A stressed coastal area. Estuarine, Coastal and Shelf Science **21**: 539-554.

Steimle, F. W. J. 1987. Benthic faunal production. *In* Georges Bank. *Edited by* R. H. Backus. MIT Press, Cambridge, Mass., pp. 310-314.

Stenson, G. B., B. P. Healey, B. Sjare and D. Wakeham. 2000. Catch-at-age of northwest Atlantic harp seals, 1952-1999. DFO Canadian Stock Assessment Secretariat Research Document 2000/79.

Stoecker, D. K., and J. M. Capuzzo. 1990. Predation on protozoa: its importance to zooplankton. Journal of Plankton Research **12**: 891-908.

Strong, K. W. 1981. Seasonal occurrence and distribution of zooplankton in waters over the Grand Banks of Newfoundland. *In* Grand Banks Oceanographic Studies. *Edited by* MacLaren Plansearch, prepared for Mobil Oil, 32 pp.

Sullivan, B. K. 1980. *In situ* feeding behavior of *Sagitta elegans* and *Eukrohnia hamata* (Chaetognatha) in relation to the vertical distribution and abundance of prey at Ocean Station 'P'. Limnology and Oceanography **25**: 317-326.

Swain, D. P., and A. F. Sinclair. 2000. Pelagic fishes and the cod recruitment dilemma in the Northwest Atlantic. Canadian Journal of Fisheries and Aquatic Sciences **57:** 1321-1325.

Tallman, R. 1991. Reduction of uncertainty caused by discarding in the fisheries of the Gulf of St. Lawrence. *In* The Gulf of St. Lawrence: small ocean or big estuary? *Edited by* J. C. Therriault. Canadian Special Publication of Fisheries and Aquatic Sciences **113**, pp. 269-275.

Tanaka, S. 1990. Estimation of the natural mortality coefficient of whales from the estimates of abundance and age composition data obtained from research catches (SC/41/O 15). Report of the International Whaling Commission **40**: 531-536.

Templeman, W. 1982. Stomach contents of the thorny skate, *Raja radiata*, from the northwest Atlantic. Journal of Northwest Atlantic Fishery Science **3**: 123-126.

Thompson, R. J., and M. Hawryluk. 1990. Physiological energetics of the snow crab, *Chionoecetes opilio*. *In* Proceedings of the International Symposium on King & Tanner Crabs. *Edited by* A. S. G. C. Program. November 1989, Anchorage, Fairbanks, Alaska, USA, Lowell Wakefield, pp. 283-293.

Threlfall, W. 1968. The food of three species of gulls in Newfoundland. Canadian Field-Naturalist **82**: 176-180.

Trites, A. W., V. Christensen and D. Pauly. 1997. Competition between fisheries and marine mammals for prey and primary production in the Pacific Ocean. Journal of Northwest Atlantic Fishery Science **22**: 173-187.

Vesin, J. P., W. C. Leggett and K. W. Able. 1981. Feeding ecology of capelin (*Mallotus villosus*) in the estuary and western Gulf of St. Lawrence and its multispecies implications. Canadian Journal of Fisheries and Aquatic Sciences **38**: 257-267.

Vézina, A. F., C. Savenkoff, S. Roy, B. Klein, R. Rivkin, J.-C. Therriault and L. Legendre. 2000. Export of biogenic carbon and structure and dynamics of the pelagic food web in the Gulf of St. Lawrence Part 2. Inverse analysis. Deep-Sea Research II **47**: 609-635.

Vinter, M. 1989. Some notes on the biology of the starry ray, *Raja radiata*, in the North Sea. As reported in Anon 1989. Report of the Multispecies Assessment Working Group. ICES Council Meeting Papers 1989/Assess **20**: 41-43.

Waiwood, K. G., J. Majkowski and G. Keith. 1980. Food habits and consumption rates of cod from the southwestern Gulf of St. Lawrence (1979). Canadian Atlantic Fisheries Scientific Advisory Committee Research Document 80/37.

Waring, G. T., D. L. Palka, P. J. Clapham, S. Swartz, M. C. Rossman, T. V. N. Cole, L. J. Hansen, K. D. Bisack, K. D. Mullin, R. S. Wells, D. K. Odell and N. B. Barros. 1999. Long-finned pilot whale (*Globicephala melas*i): Western North Atlantic Stock. U.S. Atlantic and Gulf of Mexico Marine Mammal Stock Assessments – 1999. NOAA. Woods Hole, Massachussets, U.S. Department of Commerce, National Oceanic and Atmospheric Administration, National Marine Fisheries Service, Northeast Fisheries Science Center. NMFS-NE-153: 75-85.

Warwick, R. M., C. L. George and J. R. Davies. 1978. Annual macrofauna production in a *Venus* community. Estuarine and Coastal Marine Science **7**: 215-241.

Whipple, S. J., J. S. Link, L. P. Garrison and M. J. Fogarty. 2000. Models of predation and fishing mortality in aquatic ecosystems. Fish and Fish. **1**: 22-40.

Winberg, G. G. 1956. Rate of metabolism and food requirements of fish. Fisheries Research Board of Canada Translation Series 194.

Zamarro, J. 1992. Feeding behaviour of the American plaice (*Hippoglossoides platessoides*) on the southern Grand Banks of Newfoundland. Netherlands Journal of Sea Research **29**: 229-238.